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EFFECTS OF FOREST MANAGEMENT PRACTICES ON RACCOON ECOLOGY IN A LONGLEAF PINE ECOSYSTEM

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I am submitting herewith a thesis written by Ronald Brian Kirby entitled "EFFECTS OF FOREST MANAGEMENT PRACTICES ON RACCOON ECOLOGY IN A LONGLEAF PINE ECOSYSTEM." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

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ABSTRACT

Raccoons (*Procyon lotor*) are ecological generalists common throughout a variety of habitats across their range. Although considered an economically important furbearer species in many regions, they are considered potentially important nest predators of certain species. Because raccoons may have a significant ecological impact on the landscape, it remains important to understand their ecology in a variety of ecosystems. We studied raccoon ecology in a longleaf pine ecosystem in southwestern Georgia, where little information for the species exists. Specifically, we assessed 269 daytime resting sites (i.e., refugia) associated with 31 radio-collared adult raccoons (18M, 13F) during 2014-2015 using an information theoretic approach. The top 2 predictive models included the variables tree diameter, tree type, presence of nearby hardwood, and distances to pine, hardwood, mixed forest and agriculture. However, tree type and diameter were the only informative variables, suggesting that for our study area, variables associated with the tree itself were more important than the landscape. Additionally, we evaluated raccoon home ranges and habitat selection on a study area in which longleaf pine forest restoration practices included substantial hardwood removal efforts spanning a 15-year time period (i.e. 1999 = pre-removal; 2015 = post-removal). Male raccoons maintained larger home ranges than females during both time periods, but there were no significant differences in home range size for either sex according to time period or the interaction. Raccoon habitat use differed by time period at 2 spatial scales. When selecting a home range (second-order selection), mature pine forests were selected over all other habitat features before hardwood removal.

Following hardwood removal, the only habitat selected differently was immature pine forest. When selecting habitats within the home range (third-order selection), hardwood forests were selected over all other habitat features before and after hardwood removal. Raccoons selected wetlands and primary roads differently following hardwood removal. Our findings suggest that habitat manipulation conducive to promoting longleaf pine restoration may impact raccoon populations by altering their space use.

PREFACE

We studied raccoon ecology in a longleaf pine ecosystem in southwestern Georgia. Specifically, we investigated daytime resting sites of raccoons during 2014-2015. We also compared home range and habitat selection at 2 spatial scales as related to longleaf pine restoration practices that included substantial hardwood removal efforts spanning a 15-year time period (i.e., 1999 = pre-removal; 2015 = post-removal). Chapter I describes our research about raccoon daytime resting sites and will be formatted for publication to Forest Ecology and Management. Chapter II contains our study of raccoon home range and habitat use relative to hardwood removal, and will be formatted and submitted for publication to the Journal of Wildlife Management.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER I

CHAPTER II

LIST OF FIGURES

CHAPTER II

INTRODUCTION

Restoration of the longleaf pine (*Pinus palustris*) ecosystem of the southeastern U.S. has become a conservation priority. Historically, longleaf pine trees were harvested unsustainably and often replaced by mixed hardwood species and other pine species with a shorter maturation period [e.g., loblolly (*Pinus taeda*) and shortleaf pine (*P. echinata*); Jose et al. 2006]. Current management strategies that promote longleaf pine forest restoration include prescribed burning, removal of hardwood tree species, and seedling planting (Jose et al. 2006).

Recent pine restoration strategies promote sustainable silvicultural practices that may support conservation and biodiversity while perpetuating timber harvest. Such practices may include varying stand-age structure, density, and vigor to maintain overall ecosystem health; thereby providing valuable habitat for many wildlife species (Mitchell et al. 2006). Although raccoons (*Procyon lotor*) are an ecological generalist commonly found in a variety landscapes, few studies of raccoon ecology in the fire-dependent longleaf pine ecosystem have been conducted.

Raccoons are an economically important furbearer species throughout the Southeast, but they are also a potential predator of multiple ground-nesting species (Gehrt 2003). In the unique longleaf pine forest landscape, raccoons may prey on nests of important game species such as northern bobwhite (*Colinus virginianus*; Rollins and Carroll 2001) and eastern wild turkey (*Meleagris gallopavo silvestris*; Williams and Austin 1988). Raccoons may also prey on nests of the gopher tortoise (*Gopherus polyphemus*), a keystone species in decline (Smith et al. 2013).

Researchers and managers need to understand factors affecting raccoon habitat and space use in the longleaf pine ecosystem to limit their impacts to other ecologically important species.

OBJECTIVES

The overall purpose of this study was to learn more about raccoon ecology in the longleaf pine ecosystem in which restoration practices have included substantial hardwood removal management practices that occurred over a 15-year time period (i.e., 1999 = pre-removal; 2015 = post-removal). Our findings will help managers determine whether habitat management may be used as a means to limit nest predation by altering raccoon space use. We described daytime resting sites for raccoons and evaluated habitat and space use relative to hardwood removal efforts. More specifically, the objectives were:

Objective 1. To describe habitat characteristics associated with raccoon daytime resting sites on a longleaf pine-dominated study area.

Objective 2. To compare home ranges of adult male and female raccoons before and after hardwood removal.

Objective 3. To evaluate habitat selection of adult raccoons at 2 spatial scales before and after hardwood removal.

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CHAPTER I

THE IMPORTANCE OF HARDWOOD TREES AS RACCOON DAYTIME RESTING SITES IN A LONGLEAF PINE FOREST

ABSTRACT

Raccoons (*Procyon lotor*) are a significant predator of ground-nesting species such as gopher tortoise (*Gopherus polyphemus*) and northern bobwhite (*Colinus virginianus*), both species important in longleaf pine (*Pinus palustris*) and other pine ecosystems of the southeastern U.S. In forested ecosystems, raccoons prefer hardwood-dominated habitats and removal of hardwood trees within pine forests may serve as a tool for non-lethally managing raccoon predation within these forests. We examined 269 daytime resting sites (DRS) associated with 31 radio-collared adult raccoons (18M, 13F) during 2014-2015 on a longleaf pine-dominated study site in southwestern Georgia. We developed and evaluated 26 *a priori* models using an informative theoretic approach to better understand factors affecting use of DRS by raccoons. The top 2 models (Δ AIC <2) had combined model weights of 0.75 and contained tree diameter, tree type, presence of nearby hardwood, and distances to pine, hardwood, mixed forest and agriculture as predictors. However, the only informative variables were tree type and tree diameter. Raccoons used DRS in all available forest types, but were less likely to use pine trees (n = 7) relative to hardwoods (n = 247), and there was a positive relationship with tree diameter. When comparing DRS between genders, females used smaller trees that were farther from agriculture and primary roads, and were closer to wetlands than those used by males. Removal of mature hardwoods from the longleaf pine matrix may be effective as a nonlethal means to reduce nest predation by raccoons. However, hardwoods are beneficial to other wildlife within the longleaf pine matrix, and managers must consider both cost and benefit before implementing hardwood removal from within this landscape.

INTRODUCTION

Restoration of open pine ecosystems, such as longleaf pine (*Pinus palustris*), has become a conservation priority throughout much of the southeastern United States. Longleaf pine forests are considered among the most species-rich ecosystems in North America (Walker and Peet, 1984; Hardin and White, 1989; Peet and Allard, 1993), containing nearly one-quarter of all plant species found in the U.S. and Canada (Clewell, 1986; Stein et al., 2000). Historically, longleaf pine trees were harvested unsustainably and often replaced by mixed hardwood and other pine species with a shorter maturation period [e.g., loblolly (*Pinus taeda*) and shortleaf pine (*P. echinata*); Jose et al., 2006]. Loss of habitat to more profitable land use practices (e.g., agriculture production) has resulted in declining, threatened, or endangered endemic flora and fauna associated with longleaf pine ecosystems (Kirkman and Mitchell, 2006).

Current management strategies that promote longleaf pine forest restoration include prescribed burning, mechanical removal of hardwood trees, and reforestation (Provencher et al., 2001; Kush et al., 2004; Jose et al., 2006). The most important factor for sustaining the longleaf pine ecosystem is low-intensity frequent fire (Heyward, 1939; Wahlenberg, 1946; Lemon, 1949; Hiers et al., 2000; Kirkman et al., 2004), which controls broad-leaved hardwood tree species and is necessary to sustain the diverse plant community associated with the longleaf system (Leach and Givinish, 1996; Jacqmain et al., 1999; Liu et al., 2005; Mitchell et al., 2006). Recent longleaf pine restoration efforts also include incorporation of management strategies for wildlife communities to promote overall ecosystem health (Mitchell et al., 2006).

Although raccoons (*Procyon lotor*) are an economically important furbearer, they are also a potential predator of multiple ground-nesting species (Gehrt, 2003). In longleaf and other open pine landscapes, raccoons may prey on nests of important game species such as northern bobwhite (*Colinus virginianus*; Rollins and Carroll, 2001) and eastern wild turkey (*Meleagris gallopavo silvestris*; Williams and Austin, 1988). Raccoons may also prey on nests of the gopher tortoise (*Gopherus polyphemus*), a keystone species thought to be declining throughout much of its range (Smith et al., 2013).

Raccoon habitat use in a variety of landscapes is well documented (Beasley et al., 2007; Fritzell, 1978; Chamberlain et al., 2003; Byrne and Chamberlain, 2011), but the importance of daytime resting sites (i.e., daytime refugia; Wilson and Nielsen, 2007) remains largely unstudied. Documented daytime resting sites (DRS) have included exposed ground, manmade structures, and rock crevices, but hardwood tree cavities were most preferred when available (Gehrt, 2003; Henner et al., 2004; Wilson and Nielsen, 2007). Henner et al. (2004) found that woody patch size and other macrohabitat features influenced DRS, and Wilson and Nielsen (2007) noted that finer scale habitat features such as distance to roads and water, number of nearby den sites, den height, and tree size influenced raccoon DRS. Daytime refugia characteristics for raccoons in longleaf pine ecosystems have not been studied, but hardwood trees may be especially important to raccoons within such forests where hardwood availability is limited. Understanding habitat features contributing to use of DRS may provide opportunities to limit raccoon impacts on ground nesting species within longleaf and other open pine systems.

Traditional hardwood management in fire-prone longleaf pine landscapes sometimes involves indiscriminate removal and elimination of oaks (*Quercus* spp.). However, certain oak species increase biodiversity and can have positive impacts on forest system dynamics (Hiers et al., 2014). As management and restoration of longleaf pine forests continues in the Southeast, land management strategies focusing on removal of mesophytic oak species [e.g., water oak (*Quercus nigra*) and live oak (*Q. virginiana*)] while retaining more pyrophytic oaks such as southern red oak (*Q. falcata*) and post oak (*Q. stellata*) has been suggested (Hiers et al., 2014). This suggestion has implications for raccoon ecology and may potentially affect nest predation by raccoons.

The development of an integrated pest management approach, using habitat management to influence predation rates, may provide land managers with alternatives to lethal removal of predators (Chamberlain, 1999; Rollins and Carroll, 2001). Although it has been suggested that habitat manipulation may reduce nest predation by limiting predator use, there are no data that specifically address this concept for raccoons (Chamberlain et al., 2003). Targeted hardwood removal may result in fewer suitable DRS for raccoons (Beasley and Rhodes, 2012; Owen et al., 2015), but this has not been studied in longleaf pine systems. If raccoons tend to use mesophytic oak species, removing these species while retaining pyrophytic oaks may improve biodiversity in longleaf pine forests, while also serving as a tool to indirectly manage nest predation. To determine if control of hardwoods within longleaf pine forests may affect raccoon use of DRS, we evaluated habitat characteristics associated with raccoon DRS on a longleaf pine-dominated study area.

MATERIALS AND METHODS

Study area

We conducted research at the Joseph W. Jones Ecological Research Center at Ichauway (hereafter Jones Center). The Jones Center was a privately owned, 11,735-ha research facility in southwestern Georgia. The Ichawaynochaway Creek flowed for approximately 24 km through the study area, and the Flint River served as approximately 22 km of the eastern boundary (Boring, 2001). The Jones Center was characterized by flat to gently rolling karst topography with elevation ranging from 27 to 61 m above sea level. It had annual precipitation of 132 cm and temperatures ranging from 11°C (winter) to 27°C (summer) (Boring, 2001). Longleaf pine woodlands and limesink wetlands dominated the Jones Center, with an understory predominately consisting of wiregrass (*Aristida stricta*) and old-field grasses (*Andropogon* spp.; Drew et al., 1998). In addition to longleaf pine, other *Pinus* spp. included loblolly pine, shortleaf pine, and slash pine (*Pinus elliottii*).

Prescribed burning was the primary land management practice on the Jones Center, normally performed on an approximate 2-year rotation during the dormant and growing season (1 January - 31 July). Additional practices associated with restoration and maintenance of longleaf pine ecosystems included mechanical removal of hardwoods from longleaf pine uplands. Limited hardwood removal on the study area occurred from 1993-1999 (<170 ha total) to restore the upland longleaf pine matrix. Nearly 4,000 ha of open longleaf pine forests received selective hardwood removal between 2000-2014, with a focus on mesophytic species including water oak and live oak.

However, large pyrogenic hardwood trees (e.g., southern red oaks, post oaks) were retained such that they were well interspersed within the longleaf pine matrix. Supplemental feeding, maintenance of wildlife food plots, and predator (e.g., coyote [*Canis latrans*], bobcat [*Lynx rufus*], raccoon, gray fox [*Urocyon cinereoargenteus*], and Virginia opossum [*Didelphis virginiana*]) management were used on portions of the Jones Center to promote northern bobwhite populations (Nelson et al., 2015).

We conducted research specifically on 2 sites within the Jones Center, the North Site (5,451 ha) and the South Site (2,561 ha), which were separated by large agricultural fields and 2 heavily used state highways. Although raccoons were harvested on portions of the Jones Center as part of the predator management program, lethal predator management did not occur in our study sites. While both sites were managed similarly and were dominated by mature longleaf pine forests, habitat composition differed. Using existing land cover data maintained by the Jones Center, we classified 9 habitats in each study site and determined the amount and percentage of each habitat type. The North Area contained 22% agriculture, 8% hardwood, 24% mature pine, 24% mixed pine-hardwood forest, 2% other, 8% pine regeneration, 1% river/creek, 4% shrub/scrub, and 6% wetland. The South Area contained 26% agriculture, 4% hardwood, 40% mature pine, 16% mixed pine-hardwood forest, 1% other, 8% pine regeneration, 3% river/creek, 2% shrub/scrub, and 1% wetland.

Field methods

We trapped raccoons from January-March 2014 using cage traps (Tomahawk Live Trap Co., Tomahawk, WI). We anesthetized adult raccoons using 10 mg/kg of ketamine hydrochloride (Fort Dodge Animal Health, Fort Dodge, IA; Bigler and Hoff, 1974; Kreeger and Arnemo, 2012). While animals were under anesthesia, we classified their age based on tooth wear (Grau et al., 1970) and we measured and recorded weight, gender and previous signs of lactation (i.e., reproductive characteristics; Sanderson, 1961). We placed VHF radio-collars (ATS Series M2300, Isanti, MN) on adult raccoons and allowed each animal to fully recover in a secure location prior to release at the capture site. All animal capture and handling procedures were approved under the University of Georgia IACUC (A2013 11-008-Y1-A0).

We located each radio-collared raccoon using VHF radio telemetry a minimum of 2 times per week, with >8 hours between each location to ensure biological independence. We estimated locations by triangulation using a handheld receiver and 3-element Yagi antenna (Wildlife Materials, Murphysboro, IL) from known points throughout the study area. We limited time between consecutive bearings to <15 minutes to minimize error due to animal movement between readings (White and Garrott, 1990). We collected data throughout the diel period to ensure equal sampling of raccoon locations during day and night-time periods. Radio monitoring of animals occurred for approximately 1 year. Radio-collared raccoons lost to mortality or transmitter failure were replaced with new study animals.

Daytime refugia

We assessed daytime resting sites for each radio-tagged raccoon ≥2 times per biological season (breeding [10 Feb - 9 Jun], kit-rearing [10 Jun - 9 Oct], and fall/winter [10 Oct - 9 Feb] [sensu Chamberlain et al. 2003]). We used homing (Kenward, 2001) to locate daytime resting sites during daylight hours from ≥90 minutes after sunrise until 90 minutes prior to sunset. When possible, we visually confirmed raccoon locations in their daytime resting position. We recorded a GPS location at each DRS. We classified refugia sites into 1 of 5 categories: tree cavity, exposed tree branch, brush pile, manmade structure, or exposed ground. For all tree sites, we recorded the species and diameter at breast height (DBH) of the tree using a diameter tape (Forestry Suppliers Metric Steel Tape Model 349D, Jackson, MS). For raccoons on an exposed tree branch, we measured the distance from the ground to the raccoon using a clinometer (Suunto PM5/360PC).

Using pre-existing land cover data from the Jones Center, we classified habitat into 6 types for analysis of DRS: forested/herbaceous wetland (WD), pine forest (P), hardwood forest (H), mixed pine-hardwood forest (M), agriculture/food plot (AG), and water (W). We used ArcGIS 9.3 (ESRI, Redlands, California, 2009) to identify habitat types containing DRS. We also calculated the shortest linear distance (m) from each DRS location to each of the 6 habitat types, primary roads (PR; paved and primary dirt roads) and other roads (OR; secondary and tertiary dirt/grass roads, in addition to firebreaks). In addition, tree type (TT) and diameter (TD), and presence of multiple hardwoods (i.e., >1 hardwood present within a 50 m radius; HP) were recorded to evaluate the influence of the tree itself on selection of DRS.

Because our objective was to evaluate the importance of hardwood trees, we excluded non-tree DRS from habitat analysis. For tree DRS that were used multiple times (i.e., multi-use DRS), we only included applicable trees one time for analysis. We compared diameter and height for multi-use DRS versus single-use DRS.

We generated 95% minimum convex polygon (MCP) home ranges for each raccoon that had ≥30 radio-locations and were monitored for ≥12 weeks using Home Range Tools (Rodgers et al., 2007) for ArcGIS (ESRI, Redlands, California). Using Hawth's Analysis Tools (Beyer, 2004) for ArcGIS, we generated one random point for each unique tree DRS identified per raccoon within each 95% MCP home range, and selected the nearest tree with a minimum tree diameter of 18.1 cm to measure the same variables as those recorded at DRS to serve as controls (Conner and Godbois, 2003). The minimum diameter represented the smallest tree observed for a raccoon DRS.

Data analysis

We used an information theoretic approach to data analysis (Anderson et al., 2000; Burnham and Anderson, 2002). We developed 26 *a priori* models to describe raccoon DRS that included macrohabitat (i.e., land use) and microhabitat variables (Table 1.1). We modeled type of site (DRS or random) as a function of habitat variables using logistic regression (i.e., a generalized linear model with a binomial distribution and logit link) in Program R (R Development Core Team, 2013). We also used logistic regression to assess gender-specific differences in raccoon DRS. We did not treat individual animal as random effect, preferring instead to allow individual animal preferences to impact results relative to the number of DRS obtained for each animal.

Thus, we had 2 sets of models: one predicting DRS relative to random sites and another using habitat variables to assess gender-specific differences in DRS.

We evaluated models within each set and identified important predictors using Akaike's Informaition Criteria (AIC). We calculated Akaike weights (w_i) for each model as an estimate of model support. We used adjusted weights for the top 95% of models to perform model averaging of parameter estimates and calculated weighted unconditional standard errors associated with model averaged estimates for each predictor variable (Burnham and Anderson, 2002). Parameter estimates with 95% confidence intervals that included zero were considered uninformative (Miller and Conner, 2007). We used paired *t*-tests to compare single and multi-use tree diameter and to evaluate differences by gender for raccoon DRS on exposed tree branches.

RESULTS

We located 269 DRS for 31 radio-collared adult raccoons (18 M, 13F) between 20 January 2014 and 24 January 2015; 254 DRS were in trees and 15 were classified as other [i.e., brush piles (n= 8), vegetation thickets (n = 5), down tree (n = 1) or on the ground (n = 1)]. Twenty-eight DRS sites (25 trees and 3 brush piles) were used more than once by radio-collared raccoons (i.e., multi-use sites). We identified 224 unique DRS trees (217 hardwoods and 7 pines) for use in analyses and measured habitat variables associated with an equal number of random trees for comparison.

Multi-use DRS trees either were used by different individuals or by the same individual more than one time. On 3 occasions, we found 2 radio-collared adult male raccoons in the same DRS tree, and once we found 3 radio-collared males in the same cavity. Male raccoons used 13 individual trees multiple times; 69% of those trees were independently visited by more than one male and remaining trees were visited multiple times by the same individual. We did not observe males using a DRS that was also used by a female. Females were observed using 12 individual trees multiple times, and we only observed one case of a female raccoon using a DRS previously used by another female raccoon.

The 2 best competing models (Micro and Micro + Land use; Δ AIC ≤ 2.0) included: tree type (pine or hardwood), tree diameter (cm), presence of multiple hardwoods, and distances to agriculture, hardwood, pine, and mixed pine-hardwood as predictors (Table 1.2). The combined w_i for these 2 models ($w_i = 0.75$) was >10 times greater than the next closest approximating model ($w_i = 0.07$). The top 5 models had a combined $w_i = 0.95$ and model averaging using these models suggested tree type and tree diameter were the only informative variables (i.e., confidence intervals did not include zero; Table 1.3).

Raccoons were less likely to use pine trees compared to hardwoods, and preferred large diameter trees (Table 1.3). Unique DRS trees selected by raccoons were predominantly hardwood species (97%). Most (73.6%) DRS trees were water oak and live oak, whereas random sites were primarily pine species (65.2%; *Pinus* spp.). DRS trees were larger in diameter than random trees ($\bar{x}$ = DBH 80.0 cm compared to 52.6 cm, respectively), but the difference in DBH we observed for DRS compared to random trees was conservative because small random trees (i.e., DBH $\leq$18.1 cm) were not sampled and only one trunk was measured on large mature hardwoods that forked below breast height. The global model best described differences between male and female DRS (Table 1.4). Females used smaller trees and were found farther from agriculture and primary roads than males, but female DRS were closer to wetlands than male DRS (Table1.5).

We identified 189 single use and 25 multi-use DRS trees. There was no statistical difference when comparing DBH among single ($\bar{x}$ = 76.71 cm) and multi-use ($\bar{x}$ = 90.2 cm) DRS trees (t = -1.5371, d.f. = 29.151, P = 0.1351). We identified 153 DRS on exposed tree limbs where estimated height above ground was collected ($\bar{x}$ = 12.89 m); males ($\bar{x}$ = 13.22 m) and females ($\bar{x}$ = 12.52 m) used tree limbs similar in height above ground (t = -1.0209, d.f. = 138.48, P = 0.3091).

DISCUSSION

Availability seems to strongly affect type of DRS used by raccoons. On our forest-dominated study site, 94% of DRS were in trees and ground refugia were rare, which was comparable to other studies conducted in forested areas (Stuewer, 1943; Cabalka, 1952; Berner and Gysel, 1967; Rabinowitz, 1981; Wilson and Nielson, 2007). In contrast, Ragland (2005) observed raccoons using ground DRS 52% of the time on a study site in central Kentucky dominated by pasture and grasslands, where groundhogs (*Marmota monax*) dug burrows subsequently used for DRS. Although groundhogs were not present on our study area, the presence of gopher tortoise burrows provided ample opportunities for raccoons to use burrows as ground DRS. However, we did not observe raccoons using gopher tortoise burrows, suggesting that tree DRS are preferred over ground DRS when suitable trees are available.

We found that tree type and diameter, and the presence of multiple hardwoods at a site were important predictors of DRS. Tree type and diameter were the 2 most important characteristics associated with raccoon DRS; large ($\bar{x}$ = 80.0 cm) diameter hardwood trees were important for raccoon DRS in the longleaf pine forests on our study sites. Mature hardwood trees may provide ample shade and protection from high temperatures observed in longleaf forests during spring and summer months. Likewise, Wilson and Nielsen (2007) observed that raccoons readily used tree cavities that are often associated with mature hardwood trees during the cooler months and periods of inclement weather. Thus, DRS in large hardwoods may provide raccoons with thermoregulatory benefits throughout the year.

Raccoons are largely inactive during the day (Johnson, 1970; Urban, 1970; Schneider, 1971). Presumably, DRS are chosen at least partially for safety during these periods of inactivity. The high use of tree DRS by raccoons on our study area may have been related to avoidance of coyotes (*Canis latrans;* Endres and Smith, 1993), one of the apex predators in the longleaf pine forest. Coyotes are considered a predator of raccoons in some regions of the midwestern U.S. (Hasbrouck et al., 1992; Sargeant et al., 1993) and the mesopredator release hypothesis suggests that coyotes as a top predator may suppress raccoon populations (Crooks and Soulé, 1999). Similarly, tree DRS may be particularly valuable for females during the kit-rearing season to provide added safety for young (Henner et al., 2004).

We recorded 3 occurrences during which more than one radio-collared male was in the same DRS at the same time; including one observation of three radio-collared males simultaneously sharing a DRS. Two of these events occurred during a substantial winter rain event (>11.5 cm). Schneider et al. (1971) suggested that tree characteristics influenced DRS more than tree location when protection from weather is important. Prange et al. (2011) found that males often shared den sites during winter. Observation of males using the same DRS and maintaining overlapping home range areas may also suggest formation of a coalition group, to increase mate defense (Gehrt and Fritzell, 1998; Chamberlain and Leopold, 2002; Pitt et al., 2008). In areas with high population density and grouped distribution of females, the development of a coalition group is advantageous, as it limits competition among outside individuals and increases territory maintenance (Caro, 1994; Gehrt and Fritzell, 1998; Conner and Whitehead, 2005; Prange et al., 2011). We did not observe radio-collared adult females sharing DRS with other adults of either sex. Collectively, these observations are consistent with the idea that females are more solitary than males (Gehrt and Fritzell, 1998; Pitt et al., 2008).

Raccoons' preference for large hardwood trees when selecting DRS was consistent regardless of surrounding habitat features (i.e., forest stand type). Live oak and water oak trees were prevalent throughout the study area and comprised approximately 74% of all raccoon tree DRS. Tree circumference was also important in determining DRS in southwest Illinois (Wilson and Nielsen, 2007), and our model revealed that variables associated with raccoon DRS were primarily associated with the tree itself and less affected by landscape context.

This finding differed from Wilson and Nielsen (2007), who observed that distances to nearest road and water were important when predicting raccoon DRS.

When modeling gender-specific DRS, we observed female raccoons to use smaller trees, farther from agriculture and primary roads, and closer to wetlands than males. Wilson and Nielsen (2007) found DRS trees to be smaller during kit-rearing season than random trees and trees used during the breeding season. The smaller home range sizes of female raccoons relative to males (McNab, 1963; Fritzell, 1978; Gehrt and Fritzell, 1997) suggests females may have a limited number of suitable trees relative to those available to males, and the solitary nature of females suggests they may be less likely to share higher quality, mature trees.

Food abundance may influence raccoon use of DRS according to gender. We observed that hardwoods were selected over pine, potentially because they produce nutritionally-rich acorns (Halls, 1977) that serve as a primary food source during fall and winter (Johnson, 1970; Henner et al., 2004). Male raccoon DRS were positively associated with agriculture, generally food plots, within the forested matrix. Similarly, availability of row crops and localized food sources (sensu Johnson, 1970) are known to influence raccoon movements (Schneider et al., 1971) and den selection (Henner et al., 2004). Mesophytic trees flourish in areas surrounding agriculture because of poor soil conditions (i.e. moist soils), inaccessibility, or ineffective land management practices. We frequently observed raccoons using mature mesophytic tree DRS along edges with agricultural areas, affording crop food sources during the growing season.

Water availability may also influence DRS. The global model suggested that female DRS were positively associated with wetlands. Henner et al. (2004) found that den site selection was based on food and water availability in an agricultural landscape in the Black Prairie region of Mississippi. Similarly, Gehrt and Fritzell (1998) determined that free water influenced raccoon distribution in open rangelands of south Texas.

To maintain longleaf pine-dominated landscapes managers often focus on controlling hardwood establishment within the pine-matrix (Hiers et al., 2014). Our findings suggest that mature hardwood trees are important to raccoons as daytime refugia. Removal of mature hardwoods from within open pine stands alters space use patterns in these landscapes, which may shift selection of DRS to other habitats such as forested wetlands (R. Kirby, unpublished data). Thus, hardwood removal practices may serve as an indirect means of managing raccoon predation on species nesting within upland longleaf pine forest. Importantly, this management is consistent with current restoration and management practices. However, hardwoods are beneficial to other wildlife within the longleaf pine matrix, and benefits should be considered before implementing excessive hardwood removal (Hiers et al., 2014). Because raccoons on our study area primarily used mesophytic hardwoods as DRS, management practices that focus on retaining pyrophytic oak species in fire-prone landscapes, while limiting mesophytic species, may provide a long term strategy for managing predation while sustaining ecologically important species and promoting biodiversity.

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APPENDIX I

Table 1.1. Categories and definitions for variables measured at raccoon daytime resting sites and random sites at the Joseph W. Jones Ecological Research Center at Ichauway in southwestern Georgia, USA, 2014-2015.

Category	Variable	Definition
Micro	TT	Tree type (hardwood or pine)
	TD	Diameter (cm) of refuge tree
	HP	>1 Hardwood present within 50 meters of refuge tree
Hydro	W	Distance to river/creek (m)
	WD	Distance to forested/herbaceous wetland (m)
Land Use	AG	Distance to agriculture/food plot (m)
	H	Distance to hardwood forest (m)
	M	Distance to mixed pine-hardwood forest (m)
	P	Distance to pine forest (m)
Road	PR	Distance to primary road (m)
	OR	Distance to other road (m)

Table 1.2. Landscape-level models associated with tree daytime resting site selection of raccoons at the Joseph W. Jones Ecological Research Center at Ichauway in southwestern Georgia, USA, 2014-2015.

Model[a]	K[b]	AIC[c]	ΔAIC[d]	w_i[e]
Micro (TT+TD+HP)	4	396.06	0.00	0.45
Micro + Land use (M+P+H+AG)	7	396.83	0.77	0.30
Micro + Road (PR+OR)	6	399.67	3.61	0.07
Micro + Hydro (WD+W)	6	399.71	3.65	0.07
Micro + Road + Land use	10	400.14	4.08	0.06
TT	2	401.65	5.59	0.03
Micro + Hydro + Road	8	403.37	7.31	0.01
Global	12	403.81	7.75	0.01
TD	2	549.75	153.70	0.00
Land use	5	565.18	169.10	0.00
Road + Land use	7	567.81	171.75	0.00
Hydro + Land use	7	569.04	172.98	0.00
Hydro + Road + Land use	9	571.68	175.62	0.00
H	2	585.13	189.07	0.00
HP	2	586.76	190.70	0.00
M	2	602.59	206.53	0.00
P	2	609.21	213.15	0.00

Table 1.2 continued

Model[a]	K[b]	AIC[c]	ΔAIC[d]	w_i[e]
AG	2	622.74	226.68	0.00
Null	1	623.06	227.00	0.00
W	2	624.24	228.18	0.00
PR	2	624.78	228.72	0.00
OR	2	625.06	229.00	0.00
WD	2	625.06	229.00	0.00
Hydro	3	626.24	230.18	0.00
Road	3	626.77	230.71	0.00
Hydro + Road	5	629.80	233.74	0.00

[a.] Landscape-level variables within models include tree type (TT), tree diameter (TD), >1 hardwood present (HP), and distances to forested/herbaceous wetland (WD), mixed pine-hardwood forest (M), pine forest (P), hardwood forest (H), agriculture/food plot (AG), water (W), primary road (PR), and other road (OR).
[b.] Number of variables (K).
[c.] Akaike's Information Criterion (AIC).
[d.] Distance from Akaike's Information Criterion (ΔAIC).
[e.] Model weights.

Table 1.3. Micro and Land use model averaged variables and estimates associated with tree daytime resting site selection of raccoons at the Joseph W. Jones Ecological Research Center at Ichauway in southwestern Georgia, USA, 2014-2015.

Variable[a]	β	SE	95% Lower CI	95% Upper CI
TT	-3.5750	0.4420	-4.4413	-2.7087
TD	0.0130	0.0040	0.0052	0.0208
HP	0.5167	0.5743	-0.6089	1.6422
AG	0.0000	0.0003	-0.0007	0.0006
H	-0.0010	0.0008	-0.0025	0.0006
M	-0.0018	0.0015	-0.0047	0.0011
P	-0.0011	0.0010	-0.0031	0.0010

[a.] Landscape-level variables retained in top performing models include tree type (TT), tree diameter (TD), >1 hardwood present (HP), and distances to mixed pine-hardwood forest (M), pine forest (P), hardwood forest (H), and agriculture/food plot (AG).

Table 1.4. Top-performing landscape-level models associated with tree daytime resting site selection of raccoons with gender as the response variable at the Joseph W. Jones Ecological Research Center at Ichauway in southwestern Georgia, USA, 2014-2015.

Model[a]	K[b]	AIC[c]	ΔAIC[d]
Global (TT+TD+HP+WD+M+P+H+AG+W+PR+OR)[e]	12	268.09	0.00
Micro (TT+TD+HP) + Hydro (WD+W)	6	276.40	8.31
Micro + Hydro + Road (PR+OR)	8	276.94	8.85

[a.] Landscape-level variables within models include tree type (TT), tree diameter (TD), >1 hardwood present (HP), and distances to forested/herbaceous wetland (WD), mixed pine-hardwood forest (M), pine forest (P), hardwood forest (H), agriculture/food plot (AG), water (W), primary road (PR), and other road (OR).
[b.] Number of variables (K).
[c.] Akaike's Information Criterion (AIC).
[d.] Distance from Akaike's Information Criterion (ΔAIC).
[e.] Only informative model of the 26 evaluated.

Table 1.5. Global model parameter estimates used to estimate gender of raccoons using daytime resting sites at the Joseph W. Jones Ecological Research Center at Ichauway in southwestern Georgia, USA, 2014-2015.

Variable[a]	β	SE	95% Lower CI	95% Upper CI
AG	-0.0049	0.0014	-0.0076	-0.0022
TD	-0.0144	0.0044	-0.0230	-0.0058
WD	0.0017	0.0004	0.0009	0.0025
PR	-0.0014	0.0008	-0.0030	0.0002
H	0.0012	0.0018	-0.0023	0.0047
HP	0.5712	0.9523	-1.2953	2.4377
M	0.0051	0.0038	-0.0023	0.0125
P	-0.0008	0.0030	-0.0067	0.0051
OR	-0.0096	0.0022	-0.0139	-0.0053
TT	-16.2800	826.2000	-1635.6320	1603.0720
W	-0.0003	0.0002	-0.0007	0.0001

[a.] Landscape-level variables include tree type (TT), tree diameter (TD), >1 hardwood present (HP), and distances to forested/herbaceous wetland (WD), mixed pine-hardwood forest (M), pine forest (P), hardwood forest (H), agriculture/food plot (AG), water (W), primary road (PR), and other road (OR).

CHAPTER II

HOME RANGE AND HABITAT SELECTION OF RACCOONS IN A LONGLEAF PINE FOREST BEFORE AND AFTER HARDWOOD REMOVAL IN SOUTHWESTERN GEORGIA

ABSTRACT

Although raccoons (*Procyon lotor*) occur in longleaf pine (*Pinus palustris*) forests of the southeastern U.S. and are a known predator of ground nesting birds and herpetofauna, raccoon ecology in this system has received little study. Because raccoons are often associated with hardwoods, hardwood reduction from within longleaf pine stands may provide desired upland habitat for ground nesting species while reducing habitat suitability for raccoons. To determine impacts of operational hardwood removal on raccoon home ranges and habitat selection, we compared home range sizes and evaluated habitat selection of adult raccoons in a longleaf pine forest before ($n = 35$) and after ($n = 29$) hardwood removal efforts spanning a 15-year time period. Male home ranges were larger ($P < 0.001$) than female home ranges, but home range size was not affected by hardwood removal ($P = 0.5396$). Mean home range sizes for females were 108.5 ± 11.9 ha prior to hardwood removal and 148.2 ± 30.5 ha after hardwood removal. Home ranges for males averaged 356.2 ± 55.4 ha prior to hardwood removal and were 280.9 ± 37.7 ha after; there was no period × sex interaction ($P = 0.2141$). Raccoon habitat selection was influenced by hardwood removal at second (Wilk's $\lambda = 0.29$, $P=0.021$) and third (Wilk's $\lambda = 0.34$, $P = 0.009$) orders of selection. At the 2^{nd} order of selection, raccoons had greater ($F_{1,62} = 6.80$, $P = 0.011$) affinity for immature pine stands following hardwood removal. At the 3^{rd} order of selection, raccoons had an increased affinity ($F_{1,62} = 6.85$, $P = 0.011$) for wetlands and decreased ($F_{1,62} = 5.69$, $P = 0.020$) affinity for primary roads following hardwood removal.

Mature pine was important when establishing the home range during both time periods, but other habitats (i.e., lesser roads, immature pine, hardwood, and mixed pine-hardwood) became equally as important as mature pine following hardwood removal. Within the home range, hardwood stands remained the most important habitat feature before and after hardwood removal. Our results suggest that raccoons alter their habitat selection in response to hardwood removal, which may provide managers with non-lethal alternatives to limiting raccoons as nest predators.

INTRODUCTION

Raccoons (*Procyon lotor*) are an adaptable and abundant mesocarnivore, and are found throughout much of North America. Although they are an economically important furbearer, they are also a vector for several zoonotic and livestock diseases (Atwood et al. 2009, Rosatte et al. 2010) and are considered important nest predators of ground nesting avian species (Miller and Leopold 1992, Rollins and Carroll 2001, Gehrt 2003, Schmidt 2003) and herpetofauna (Burke et al. 2005, Smith et al. 2013). Because raccoons may have a significant ecological impact on the landscape, it is important to understand factors affecting their habitat selection and space use.

Raccoon home ranges have been studied in diverse ecosystems from agricultural systems (Beasley et al. 2007, Atwood et al. 2009) and prairies (Fritzell 1978, Henner et al. 2004) to managed pine forests (Chamberlain et al. 2002, Chamberlain et al. 2003) and urban areas (Prange et al. 2004, Bozek et al. 2007). Home range location and size is influenced by habitat, availability of food resources, presence of suitable den sites, and breeding opportunities (Gehrt 2003).

Raccoon home range size also varies between sexes and among seasons; males generally maintain larger home ranges than females, particularly during the breeding season, to maximize mating opportunities (Gehrt and Fritzell 1997, Chamberlain et al. 2003, Fisher 2007).

Habitat selection also varies based on resource availability (Chamberlain et al. 2002, Byrne and Chamberlain 2011). Across forested landscapes, hardwood forests are important to raccoons, presumably because these habitats provide den sites and hard mast during winter (Gehrt 2003). Although pine-dominated landscapes have historically been considered poor habitat for raccoons, Chamberlain et al. (2003) found that mature pine stands were equally as important to raccoons as mature hardwood habitats on a mixed pine-hardwood-dominated study area in central Mississippi. Likewise, in intensively managed pine forests in Mississippi, mature pine and pine-hardwood habitats were important to raccoons likely because lack of fire resulted in dense understory vegetation and availability of soft mast (Chamberlain et al. 2002).

Open canopied fire-dependent pine (*Pinus* spp.) forests were once ubiquitous throughout much of the Southeast. Native longleaf pine (*Pinus palustris*) ecosystems, perhaps a prototypical open-canopied pine forest type, once occupied more than 36 million ha of the Southeast, but unsustainable harvest and forest conversion to agriculture and faster-growing pine species ultimately resulted in this species occupying <5% of its former range (Landers et al. 1995, Van Lear et al. 2005, Jose et al. 2006). As such, restoration of longleaf pine ecosystems has become a conservation priority (Van Lear et al. 2005, Outcalt and Brockway 2010).

Commonly used management practices within longleaf pine forests include prescribed fire (Landers et al. 1995), mechanical removal of hardwoods (Provencher et al. 2001; Kush et al. 2004), and the use of herbicides (Brockway and Outcalt 2000). Land management strategies focusing on removal of mesophytic oak species [e.g., water oak (*Quercus nigra*) and live oak (*Q. virginiana*)] while retaining more pyrophytic oaks such as southern red oak (*Q. falcata*) and post oak (*Q. stellata*) have been suggested to promote biodiversity and positively impact forest system dynamics in the longleaf pine matrix (Hiers et al. 2014). These changes in forest composition have implications for raccoon ecology and may ultimately affect population dynamics of ground-nesting species associated with longleaf pine uplands such as northern bobwhite (*Colinus virginianus*; Rollins and Carroll 2001) and eastern wild turkey (*Meleagris gallopavo silvestris*; Williams and Austin 1988). However, raccoon ecology has received little study in longleaf pine landscapes.

Because raccoons are often associated with hardwoods and waterways (Leberg and Kennedy 1988, Gehrt and Fritzell 1998), management and restoration of longleaf pine ecosystems may provide desired upland habitat for ground nesting species while reducing habitat suitability for raccoons, subsequently reducing raccoon predation on ground nesting species. Raccoons concentrate their space use based on availability of resources, but few studies have examined the effects of forest management practices on raccoon home range size and habitat selection, especially relative to longleaf pine forests.

Jones et al. (2004) suggested that prescribed burning may reduce raccoon use for up to 2 years following fire, but no studies have evaluated effects of hardwood removal on raccoon ecology.

To determine the impacts of operational hardwood removal on raccoon home ranges and habitat selection, we studied raccoon ecology in a longleaf pine forest before and after hardwood removal efforts spanning a 15-year time period (i.e. 1999 = pre-removal; 2015 = post-removal). Specifically, we compared home range sizes of adult raccoons and evaluated habitat selection before and after hardwood removal. We hypothesized that hardwood removal would result in altered space use by raccoons as they changed behavior to take advantage of the more limited, yet preferred, resource.

MATERIALS AND METHODS

Study Area

We conducted research at the Joseph W. Jones Ecological Research Center at Ichauway (hereafter Jones Center), approximately 45 km south of Albany, Georgia. The Jones Center was a privately owned, 11,735-ha research facility in southwestern Georgia that previously served as a hunting plantation managed for northern bobwhite and other game species for over 80 yrs. (Jacqmain et al. 1999). The Ichawaynochaway Creek flowed for approximately 24 km through the study area, and the Flint River served as approximately 22 km of the eastern boundary (Boring 2001). The Jones Center was characterized by flat to gently rolling karst topography with elevation ranging from 27 to 61 m above sea level. It had annual precipitation of 132 cm and temperatures ranging from 11°C in winter to 27°C in summer (Boring 2001).

Longleaf pine woodlands and limesink wetlands dominated the Jones Center, with an understory predominately consisting of wiregrass (*Aristida stricta*) and old-field grasses (*Andropogon* spp.; Drew et al. 1998). In addition to longleaf pine, other *Pinus* spp. included loblolly pine (*P. taeda*), pond pine (*P. serotina*), shortleaf pine (*P. echinata*), and slash pine (*P. elliottii*).

Prescribed burning was the primary land management practice on the study area, normally performed on an approximate 2-year rotation with most burns occurring between 1 January-31 July, encompassing both dormant and growing season fires. Additional management practices included mechanical removal of mesophytic hardwood species such as water oak and live oak from longleaf pine uplands. Supplemental feeding, maintenance of wildlife food plots, and lethal predator (e.g., coyote [*Canis latrans*], bobcat [*Lynx rufus*], raccoon, gray fox [*Urocyon cinereoargenteus*], and Virginia opossum [*Didelphis virginiana*]) management were used on portions of the study area to promote northern bobwhite populations (Nelson et al. 2015).

Limited hardwood removal on the study area occurred from 1993-1999 (<170 ha total) to restore the upland longleaf pine matrix. Nearly 4,000 ha of open pine forests received selective hardwood removal between 2000-2014 (Figure 2.1) to increase biodiversity, facilitate recruitment of species of concern (i.e. red-cockaded woodpecker [*Leuconotopicus borealis*] and gopher tortoise), and restore the open pine forest. The primary roads on our study area were mostly dirt roads that often served as firebreaks. Firebreaks create fire shadows that have been associated with higher mast and hardwood stem density because oak species in these areas survive low-intensity fires near the ignition point (Lashley et al. 2014). Fire shadows were removed through hardwood reduction efforts, and following selective removal of hardwoods, land management reverted to a standard management regime of frequent prescribed fire implemented on a 2-year rotation and use of herbicides when needed. However, large pyrogenic hardwood trees (e.g., southern red oaks, post oaks) were retained such that they were well interspersed within the longleaf pine matrix.

Animal Capture and Monitoring

We trapped raccoons from January-March 2014 using cage traps (Tomahawk Live Trap Co., Tomahawk, WI) and anesthetized them using 10 mg/kg of ketamine hydrochloride (Fort Dodge Animal Health, Fort Dodge, IA; Bigler and Hoff 1974, Kreeger and Arnemo 2012). While raccoons were under anesthesia, we classified their age based on tooth wear (Grau et al. 1970) and reproductive characteristics (Sanderson 1961). We placed VHF radio-collars (ATS Series M2300, Isanti, MN) on adult (i.e., $\geq$1 year old) raccoons and allowed each raccoon to fully recover in a secure location prior to release at the capture site. All raccoon capture and handling procedures were approved under the University of Georgia Institutional Animal Care and Use Committee (Protocol Number A2013 11-008-Y1-A0).

Within 24 hours after release, we located each radio-collared raccoon using VHF radio telemetry a minimum of 2 times per week, with >8 hours between each location to ensure biological independence. We estimated locations by triangulation, using a handheld receiver and 3-element Yagi antenna (Wildlife Materials, Murphysboro, IL) from known points throughout the study area.

We limited time between consecutive bearings to <15 minutes to minimize error due to animal movement between readings (White and Garrott 1990). We collected data throughout the diel period to ensure equal sampling of raccoon locations during day and nighttime periods. Radio monitoring of most raccoons occurred for approximately 1 year from February 2014-February 2015.

Data Analysis

Our data analyses included data collected during 1999-2000 (Jones 2001, Storey 2001), prior to operational hardwood removal, and during 2014-2015 following removal. We used LOAS 4.0 (Ecological Software Solutions, LLC) to convert triangulated raccoon locations collected during both study periods (1999, 2015) into Universal Transverse Mercator (UTM) coordinates for analysis. We generated 95% minimum convex polygon (MCP) home ranges for each raccoon that had ≥30 radiolocations and were monitored for ≥12 weeks using Home Range Tools (Rodgers et al. 2007) for ArcGIS (ESRI, Redlands, California). We used a 2-way analysis of variance (ANOVA) to compare home range sizes relative to sex (M or F) and period (before or after hardwood reduction).

We analyzed raccoon habitat selection at Johnson's (1980) 2nd (i.e., selection of home range within the study area) and 3rd (i.e., selection of habitats within an individual's home range) orders using distance-based methods (Conner and Plowman 2001, Conner et al. 2003, Benson 2013). We defined the study area during each period by developing a 100% MCP comprised of the calculated 95% MCP home ranges for all raccoons monitored during each period. We used National Land Class Data (NLCD 2001; 2011) in conjunction with existing habitat layers (Jones Center 1997; 2015) for the study area during each time period to reclassify habitat features relevant to raccoons in ArcGIS 9.3 (ESRI, Redlands, California, 2009). We classified habitat into 9 types (Table 2.1) for purposes of analysis: agriculture/food plot (AG), hardwood forest (HW), mixed-pine hardwood forest (MF), mature pine forest (MP), immature pine forest (IP), developed/barren (DB), river/creek (RC), scrub/shrub (SS), and forested and herbaceous wetland (WL). Additional features of interest were primary roads (PRD; paved and primary dirt roads) and lesser roads (LRD; secondary and tertiary dirt/grass roads, in addition to firebreaks).

Following Benson (2013), we created distance raster layers with 10 x 10 m cells for each habitat feature using the Euclidean Distance tool in ArcGIS 10.2. Each cell in the raster layers provided the Euclidean distance to the nearest cell of the given habitat feature. We extracted distances from each habitat to each raccoon location and home range, and period-specific study areas. For analysis at the 2nd order of selection, we created a distance ratio (mean observed distance/mean expected distance) for each raccoon using the mean distances to each habitat within the home range (i.e., observed) relative to the mean distances in the period specific-study area (i.e., expected). For the 3rd order of selection, we created a distance ratio for each raccoon using the mean distances from each habitat type to the raccoon's locations (i.e., observed) relative to the mean distance to each habitat type within the raccoon's home range (i.e., expected). A habitat distance ratio <1.0 indicated the raccoon was closer than expected to that habitat type (i.e., selection) at that scale of selection, whereas a distance ratio >1.0 indicated the raccoon was farther than expected from a given habitat type (i.e., avoidance; Conner and Plowman 2001, Conner et al. 2003, Benson 2013).

We used a multivariate analysis of variance (MANOVA) to test the hypothesis that observed distances to habitats did not differ from expected distances or by period (i.e., before and after hardwood removal) as described by Conner and Plowman (2001) and Conner et al. (2003) at the 2^{nd} and 3^{rd} orders of selection. If the habitat distance ratios differed from a vector of 1's and there was a significant period effect (direct effect for period significant at $P < 0.05$), we then conducted an ANOVA on each distance ratio to test if distance ratios differed by period. We used univariate t-tests on each distance ratio for each habitat feature during each period to identify which distance ratios differed from 1. We created a habitat ranking matrix using univariate paired t-tests between each combination of habitat features for each period at each order of selection to rank habitat types in order of preference (Conner and Plowman 2001, Conner et al. 2003, Benson 2013). We performed all statistical analyses using Program R (R Core Team 2013).

RESULTS

Home Range

We used 6,000 telemetry locations for 35 radio-collared adult raccoons (13 F, 22 M) collected between March 1999 and August 2000, and 3,179 telemetry locations collected on 29 radio-collared adult raccoons (13 F, 16 M) between February 2014 and February 2015.

The number of radiolocations used to estimate home range sizes prior to hardwood removal ranged from 89 to 263 ($\bar{x}$ = 181.3 $\pm$ 20.2) for females and from 71 to 267 ($\bar{x}$ = 165.6 $\pm$ 13.5) for males. After hardwood removal, the number of radiolocations used to estimate home range sizes ranged from 40 to 145 ($\bar{x}$ = 121.2 $\pm$ 7.6) for females and from 31 to 147 ($\bar{x}$ = 100.2 $\pm$ 10.9) for males.

There was no period × sex interaction (P = 0.214), and home ranges did not differ by period (P = 0.5396). However, male home ranges were larger (P < 0.001) than female home ranges. Female home ranges ranged from 41 ha to 184 ha ($\bar{x}$ = 108.5 $\pm$ 11.9) prior to hardwood removal and from 39 ha to 439 ha ($\bar{x}$ = 148.2 $\pm$ 30.5) after (Figure 2.2). Home ranges for males ranged from 134 ha to 1216 ha ($\bar{x}$ = 356.2 $\pm$ 55.4) prior to hardwood removal and 74 ha to 645 ha ($\bar{x}$ = 280.9 $\pm$ 37.7) after (Figure 2.2).

Habitat Selection

Raccoon habitat selection differed by period at both the 2nd (Wilk's λ =0.29, P=0.021) and 3rd (Wilk's λ = 0.34, P=0.009) orders of selection. Raccoons established home ranges nearer to immature pine forest than would be expected following hardwood removal, whereas before hardwood removal raccoons established home ranges as expected regarding this habitat feature ($F_{1,62}$ = 6.80, P = 0.011). Within the home range, raccoons increased selection of wetlands ($F_{1,62}$ = 6.85, P = 0.011) and decreased selection of primary roads ($F_{1,62}$ = 5.69, P = 0.020) following hardwood removal. Results from paired comparisons indicated the ranking of habitats changed at both orders of selection following hardwood removal (Table 2.2).

Prior to hardwood removal, at the 2nd order of selection raccoons were closer than expected to mature pine forest, lesser roads, hardwood forest, mixed pine-hardwood forest, primary roads, and scrub/shrub (Table 2.3). They were as near as expected to all other habitat features. Mature pine forests were selected (i.e., nearer relative to expectation) over all other habitat features before hardwood removal (Table 2.2). Post-removal, raccoons were closer than expected to lesser roads, mature pine forest, immature pine forest, hardwood forest, and mixed pine-hardwood forest (Table 2.3). They were near as expected to wetland, primary roads, developed/barren, river/creek, and scrub/shrub, but were further than expected from agriculture.

At the 3rd order of selection, raccoons were closer than expected to hardwood forest, primary roads, river/creek, and developed/barren prior to hardwood removal (Table 2.3). They were farther than expected from mature pine and agriculture, but were near as expected to other habitat features. Following hardwood removal, raccoons were closer than expected to hardwood forest, wetland, and river/creek (Table 2.3), but as near as expected to all other habitats. Hardwood forests were selected over all other habitat features within the home range before and after hardwood removal (Table 2.2).

DISCUSSION

Our results suggest that forest management practices that manipulate resources (i.e., food or cover) for predators can influence their space use. Lethal control of predators is controversial and often ineffective (Conner and Morris 2015). An indirect benefit to ecosystem restoration techniques, such as hardwood removal in longleaf pine-dominated uplands, may be reduced predation on ground-nesting species of economic and ecological value within that ecosystem. The removal of fire shadows (i.e., areas where the fire was of insufficient severity to top-kill hardwood species) and reduction of hardwoods within the longleaf matrix appears to have altered the spatial ecology of raccoons. In general, raccoons used areas where hardwood removal occurred less (i.e., road-side fire shadows) and increased selection for areas where hardwoods were retained (i.e., forested wetlands). We suggest that hardwood removal may alter the spatial distribution of raccoons across a longleaf pine ecosystem, providing evidence that habitat manipulation may be a valuable tool for nonlethal management of raccoons in pine-dominated ecosystems.

Contrary to our hypothesis, home range sizes were not affected by hardwood removal from within the longleaf pine matrix. Chamberlain et al. (2004) found that raccoons maintained smaller home ranges within an intensively managed loblolly pine forest compared to a less intensively managed forest, suggesting that presence of hardwoods may have affected raccoon home range size. Our findings suggest that if hardwood removal resulted in declines in habitat quality for raccoons on our study site, the effect was more likely manifested in raccoons shifting their home ranges through time, as opposed to increasing home range size.

Previous studies have noted that male raccoons maintain larger home ranges than females (Johnson 1970, Sanderson 1987, Gehrt and Fritzell 1997, Chamberlain et al. 2003); hence we were not surprised to observe similar trends. Intersexual differences among raccoon home ranges are influenced by mating opportunities and availability of den sites (Gehrt and Fritzell 1997, Gehrt 2003).

Adult male raccoons are physically larger than females (Johnson 1970, Kaufmann 1982, Ritke and Kennedy 1993) and maintain larger home ranges to meet greater energetic requirements (McNab 1963). Additionally, home ranges of males may be influenced by spatial distribution of females (Gehrt and Fritzell 1998) and attempts of males to maximize breeding opportunities. Raccoon home ranges during our study area fell well within previously reported home range estimates (4 – 2,560 ha; Gehrt 2003) and were consistent with other studies conducted within southern pine-dominated landscapes (Walker and Sunquist 1997, Chamberlain et al. 2003, Fisher 2007). We present the first estimates of raccoon home range size within a predominately longleaf pine-dominated study site.

Similar to other studies of raccoons in southeastern pine-dominated forests, we found that mature pine, hardwood, and mixed pine-hardwood were important to raccoons when selecting home ranges (Chamberlain et al. 2002, Chamberlain et al. 2003), and these habitats were selected before and after hardwood removal occurred. Raccoons established home ranges closer than expected to immature pine stands following hardwood removal; immature pine stands were more prevalent after hardwood removal and were dominated by regenerating longleaf stands planted for restoration efforts. On our study area prescribed fire typically did not occur in immature pine stands for at least 1-2 years following planting, until the trees were capable of withstanding a burn (B. Rutledge, personal communication). In the absence of fire, immature pine stands became dominated with herbaceous species and soft mast, which are important food sources for raccoons (Johnson 1970).

We found that mature pine was selected by raccoons at the 2nd order over all other habitats prior to hardwood removal. However, other habitats (i.e., lesser roads, immature pine, hardwood, and mixed pine-hardwood) became equally as important as mature pine following hardwood removal, presumably because hardwoods were less available and raccoons likely shifted habitat selection to encompass habitats containing hardwoods. Raccoons used mature pine more than expected during both time periods at the 2nd order likely because this habitat feature dominated the landscape and it would be difficult to move among habitat types without encountering mature pine stands. Additionally, prescribed fire used to manage mature pine stands for red-cockaded woodpeckers encourages herbaceous vegetation and may improve environments for small mammals (Masters et al. 1998) and invertebrates (Madison et al. 1995), both food resources used by raccoons (Johnson 1970).

We observed increased selection of wetland habitat at the 3rd order following hardwood removal, likely due to the availability of mesophytic hardwood trees associated with moist soils retained in these habitats. Reduction of available hardwoods throughout the study area likely increased the value of remaining hardwoods found in forested wetlands. Raccoons are more likely to use mesophytic trees for daytime refugia (Kirby, unpublished data) because structurally they are more likely to possess cavities for denning opportunities, and because of their association with water sources. Wetlands also provide ample food sources (Fritzell 1978, Byrne and Chamberlain 2011) and have been identified as a critical resource to raccoons (Beasley and Rhodes 2010).

Notably, wetlands were selected less than hardwood, mixed pine-hardwood, river/creek, developed/barren and immature pine prior to hardwood removal. After hardwood removal, raccoons selected wetlands to all other habitats except for hardwood, and equally to mixed pine-hardwood, further emphasizing the significance of wetland habitats once hardwoods became limited in mature pine stands.

Raccoons decreased selection of primary roads within the home range following hardwood removal. The primary roads on our study area were mostly dirt roads that often served as firebreaks. Firebreaks often create fire shadows that have been associated with higher mast and hardwood stem density because species such as oaks found along these areas are subject to low-intensity fires near the ignition point; these fires are less successful at top-killing hardwood species (Lashley et al. 2014). In addition to providing concentrated food resources, roads and similar openings can be important travel corridors for raccoons (Byrne and Chamberlain 2011). During hardwood removal efforts, areas along firebreaks that contained fire shadows were specifically targeted; hence the loss of hardwood cover likely deterred raccoon use of primary roads after hardwood removal.

Raccoons significantly preferred hardwood habitat to all other habitat types during both periods at the 3rd order. Hardwood and river/creek habitats were the only 2 habitat features consistently selected by raccoons within the home range before and after hardwood removal, reiterating the importance of these habitats. Conversely, mature pine forest was not selected within home ranges and mixed pine-hardwood habitats were used as expected within the home range. Fire return intervals within mature pine stands were on a 2-year rotation, which limits growth of soft mast species used by raccoons such as blackberry (*Rubus* spp.) and American beautyberry (*Callicarpa americana*) (Johnson and Landers 1978). Likewise, hardwood removal efforts within mature pine stands focused on mesophytic species, whereas pyrophytic species were retained on the landscape because they are an important component of the longleaf pine forest (Hiers et al. 2014). Pyrophytic species were not as important to raccoons as mesophytic trees when selecting daytime resting sites within the longleaf pine-dominated study site (Kirby, unpublished data), suggesting that this forest management strategy may influence raccoon habitat selection.

Raccoons selected habitat at both 2nd order (home range) and 3rd order (within the home range). Although raccoons exploit resources within open pine landscapes, hardwood habitats remain most important at multiple spatial scales (Chamberlain et al. 2002). Habitat rankings changed at both spatial scales following hardwood removal, indicating hardwood removal may have altered habitat use by raccoons on our study area. We suggest hardwood removal from the longleaf pine matrix is the best explanation for the observed differences in habitat selection, but acknowledge that hardwood removal and sample period were confounded. Regardless, before-after studies remain common in the literature and we can think of no other environmental explanation for observed differences in habitat selection.

MANAGEMENT IMPLICATIONS

Predation, habitat loss, and fragmentation have been identified as causes leading to declines in ground nesting species (Speake 1980, Brennan 1991, Butler and Sowell 1996, Rollins and Carroll 2001).

Although traditional predation management involves lethal control, other management strategies include habitat manipulation to manage predators indirectly (Errington 1934, Jiménez and Conover 2001, Rollins and Carroll 2001, West and Messmer 2004). Carroll et al. (2007) explicitly suggested predator management should include altering habitat to make it less favorable for predators.

Numerous studies have noted effectiveness of managing for areas of dense nesting cover (e.g., scrub/shrub) to increase nest success of ground nesting birds (Lokemoen 1984, Baldassarre and Bolen 1994, Reynolds et al. 2001). Providing heterogeneous dense patches of vegetation within the landscape increases time spent by predators searching for prey, thereby decreasing predator efficiency (Bowman and Harris 1980). Several studies have suggested that predator abundance and composition can be altered by removing den sites and brush in areas where nest predation is high (Fleske and Klaas 1991, Herkert 1994, Greenwood et al. 1995).

Our findings suggest that operational hardwood removal affected raccoon space use, which may influence nest predation on ground nesting species. Following hardwood removal, raccoons established home ranges farther from agriculture and primary roads, but closer to wetlands. These changes in space use should result in decreased encounters with ground nests in mature pine stands, which were selected prior to hardwood removal. As a result, hardwood removal may be a viable management tool for increasing nest survival in some species. However, we caution that hardwoods are important to other species within the longleaf matrix (Perkins et al. 2008, Heirs et al. 2014).

Thus, indiscriminate hardwood eradication from within longleaf forests should be avoided if the goal includes balanced management for ground nesting birds and maintenance of biodiversity. The species composition, number, size, and spatial distribution of hardwoods within the longleaf matrix promises to be a rewarding area of research.

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APPENDIX II

Table 2.1. Categories for habitat features classified for raccoon home range and habitat use analysis at the Joseph W. Jones Ecological Research Center at Ichauway in southwestern Georgia, USA, 1999 and 2015.

Variable	Definition
AG	Distance to agriculture/food plot (m)
HW	Distance to hardwood forest (m)
MF	Distance to mixed pine-hardwood forest (m)
MP	Distance to mature pine forest (m)
IP	Distance to immature pine forest (m)
DB	Distance to developed/barren (m)
RC	Distance to river/creek (m)
SS	Distance to scrub/shrub (m)
WL	Distance to wetland (m)
LRD	Distance to lesser road (m)
PRD	Distance to primary road (m)

Table 2.2. Ranking matrix from pairwise comparisons of habitat types at 2nd and 3rd orders of selection for raccoons at the Joseph W. Jones Ecological Research Center at Ichauway in southwestern Georgia, USA, 1999 and 2015. Habitats with the same letter did not differ based on paired t-tests (P >0.05).

2nd Order				3rd Order			
Before		After		Before		After	
MP	A	LRD	A	HW	A	HW	A
LRD	B	MP	A	PRD	B	WL	B
HW	B	IP	A	RC	B	MF	B,C
MF	C	HW	A	MF	B	RC	C
PRD	D	MF	A,B	DB	B	LRD	C
SS	D	PRD	A,B,C	IP	C	DB	C
RC	D	WL	B,C	WL	D	IP	C
IP	D	DB	B,C	SS	E	PRD	C
WL	D	RC	C	LRD	F	AG	C
DB	D	SS	C,D	MP	G	SS	C
AG	D	AG	D	AG	G	MP	C

[a] Habitat features include agriculture/food plot (AG), hardwood forest (HW), mixed pine-hardwood forest (MF), mature pine forest (MP), immature pine forest (IP), developed/barren (DB), river/creek (RC), scrub/shrub (SS), forested/herbaceous wetland (WL), lesser road (LRD), and primary road (PRD).

Table 2.3. Results from habitat selection analysis at 2nd and 3rd orders of selection for raccoons before (i.e., 1999-2000) and after (i.e., 2014-2015) hardwood removal at the Joseph W. Jones Ecological Research Center in southwestern Georgia, USA. Shown are P-values and conclusions from t-tests that examined which habitat features were selected and avoided at α=0.05.

	2nd Order				3rd Order			
	Before		After		Before		After	
[a]	P	Conclusion	P	Conclusion	P	Conclusion	P	Conclusion
AG	0.185	NS[b]	0.019	Avoided	0.005	Avoided	0.771	NS
HW	<0.001	Selected	<0.001	Selected	<0.001	Selected	<0.001	Selected
MF	<0.001	Selected	0.001	Selected	0.109	NS	0.384	NS
MP	<0.001	Selected	0.017	Selected	0.004	Avoided	0.137	NS
IP	0.950	NS	0.004	Selected	0.259	NS	0.786	NS
DB	0.384	NS	0.841	NS	0.044	Selected	0.770	NS
RC	0.447	NS	0.626	NS	0.042	Selected	0.034	Selected
SS	0.045	Selected	0.472	NS	0.998	NS	0.375	NS
WL	0.770	NS	0.499	NS	0.326	NS	<0.001	Selected
LRD	<0.001	Selected	<0.001	Selected	0.169	NS	0.631	NS
PRD	0.041	Selected	0.340	NS	0.004	Selected	0.523	NS

a. Habitat features include agriculture/food plot (AG), hardwood forest (HW), mixed pine-hardwood forest (MF), mature pine forest (MP), immature pine forest (IP), developed/barren (DB), river/creek (RC), scrub/shrub (SS), forested/herbaceous wetland (WL), lesser road (LRD), and primary road (PRD).
b. NS indicates feature was not selected.

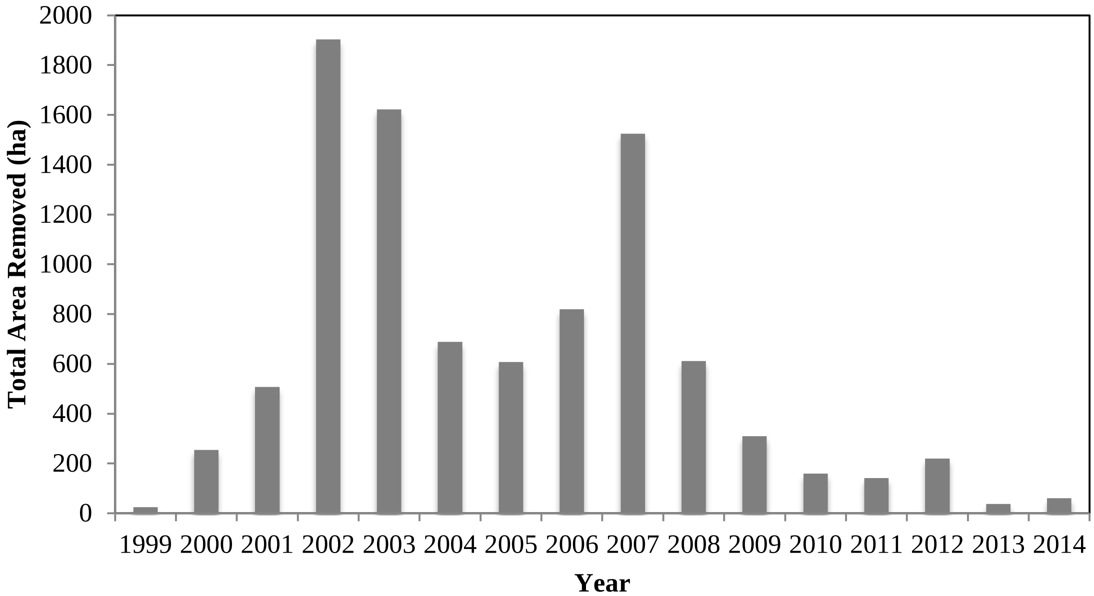

Figure 2.1. Annual total area (ha) of hardwood tree removal for longleaf pine forest restoration on the Joseph W. Jones Ecological Research Center at Ichauway in southwestern Georgia, USA, 2000-2014.

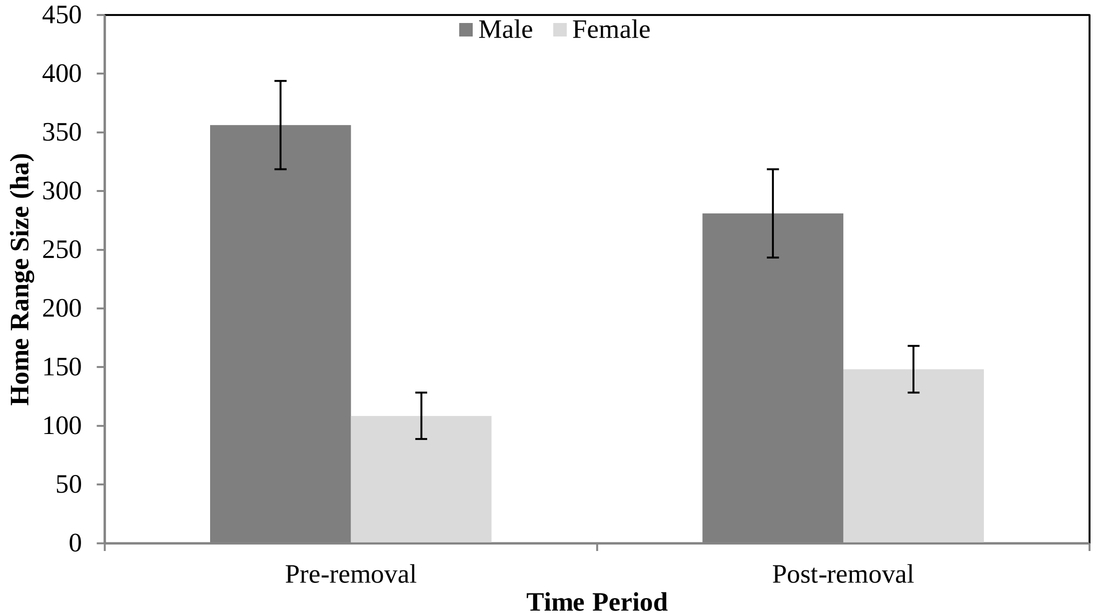

Figure 2.2. Mean home range sizes for male and female raccoons before (1999) and after (2015) selected hardwood removal on the Joseph W. Jones Ecological Research Center at Ichauway in southwestern Georgia, USA.

CONCLUSION

Raccoons commonly occur in longleaf pine-dominated forests of the southeastern U.S. and are a known predator of ground nesting birds and herpetofauna, but raccoon ecology in this system has received little study. Understanding factors that affect raccoon habitat and space use in the longleaf pine ecosystem may assist managers with limiting their impacts to other ecologically important species. Thus, we described habitat features associated with daytime resting sites (DRS), and evaluated whether forest management practices (specifically hardwood removal) affected home range size and habitat use at 2 spatial scales on a longleaf pine-dominated study area.

To maintain longleaf pine-dominated landscapes managers often focus on controlling hardwood establishment within the pine-matrix. Our findings suggested that mature hardwood trees were important to raccoons as DRS. Removal of mature hardwoods from within open pine stands alters space use patterns in these landscapes, which may shift selection of DRS to other habitats such as forested wetlands. Importantly, this strategy is consistent with current restoration and management practices. Because raccoons on our study area primarily used mesophytic hardwoods as DRS, management practices that focus on retaining pyrophytic oak species in fire-prone landscapes, while limiting mesophytic species, may provide a long term strategy for managing predation while sustaining ecologically important species and promoting biodiversity.

Hardwood removal practices may serve as an indirect means of managing raccoon predation on species nesting within upland longleaf pine forest by concentrating raccoon space use in non-upland areas. Our data indicated operational hardwood removal affected raccoon habitat use both when selecting habitats to include in the home range and when selecting habitats within the home range. Following hardwood removal raccoons established their home ranges farther from agriculture and primary roads. They were located closer to wetlands within their home ranges following hardwood removal. These changes in space use should result in decreased encounters with ground nests in the longleaf pine uplands. As a result, hardwood removal may be a viable management tool for increasing nest survival in some species. However, we caution that hardwoods are important to other species within the longleaf matrix. Thus, indiscriminate hardwood eradication from within the longleaf forest should be avoided if the goal includes balanced management for ground nesting species such as northern bobwhite and maintenance of biodiversity. The species composition, number, size, and spatial distribution of hardwoods within the longleaf matrix promises to be a rewarding area of research.

VITA

Ronald Brian Kirby was born in Farmville, North Carolina in 1980, but spent much of his childhood outside of Savannah, Georgia. Brian received his Bachelor of Science in Forest Resources (Emphasis in Wildlife) from the Warnell School of Forestry and Natural Resources at the University of Georgia in 2003. He began his career in wildlife as a research technician at the Joseph W. Jones Ecological Research Center at Ichauway in southwestern Georgia during 2004. The following year, Brian became a Wildlife Specialist for the USDA, APHIS, Wildlife Services program in Louisville, Kentucky. Brian worked for the next 8.5 years on a variety of wildlife damage management projects in Kentucky and Tennessee, including raccoon rabies management activities and completion of a comprehensive Wildlife Hazard Assessment for the Air National Guard at McGhee-Tyson Airport in Knoxville, Tennessee. In 2013, Brian accepted a research assistantship through the University of Tennessee in collaboration with the Joseph W. Jones Ecological Research Center and the University of Georgia to study raccoon ecology in the longleaf pine system. He received his Master of Science degree in Wildlife and Fisheries in December 2015.