ABSTRACT

GARABEDIAN, JAMES EDWARD. Population-density Mediated Resource Partitioning by Foraging Red-cockaded Woodpeckers. (Under the direction of Christopher E. Moorman and Markus N. Peterson)

The red-cockaded woodpecker (*Leuconotopicus borealis*; RCW) is endemic to pine (*Pinus* spp.) forests of the southern USA and listed as federally endangered. Loss of habitat, particularly longleaf pine (*P. palustris*) forests and old pines required for nesting and roosting, was the primary historic cause of the species' decline. As nesting constraints are now mitigated through techniques such as prescribed burning and artificial cavity construction, foraging habitat management has gained importance in recovery of the species. Despite the central role in foraging habitat quality in the species' recovery, documented relationships between RCW fitness and foraging habitat guidelines described in the species' current recovery plan are inconsistent and weak. Advances in remote sensing and global positioning systems technology offer new tools for collection of data on RCW space use and response to fine-grained foraging habitat structure. We collected home-range data for 44 groups between April 2013 and March 2015 on two sites, the Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina, USA, by visually tracking neighboring RCW groups as they foraged throughout the day. We used fine-grained light and distance ranging (LiDAR) derived estimates of United States Fish and Wildlife Service recovery plan habitat attributes and utilization distributions (UDs) to evaluate and rank selection of alternative foraging habitat thresholds for RCW recovery on the Savannah River Site (Chapter 1). We used UDs and behavioral observations on Savannah River Site and Carolina Sandhills National Wildlife Refuge to determine whether neighboring groups shared foraging habitat to the same degree across a range of density conditions or whether groups instead reduced their home range size as density increased (Chapter 2). We also investigated

how changes in space use and density influence group fitness and discuss implications for critical habitat delineation. We used the LiDAR-derived structural habitat thresholds and multiscale effects of territorial behaviors, cavity trees, and population density to develop a fine-grained model of space use to guide strategic management of RCWs (Chapter 3). In contrast to the current range-wide United States Fish and Wildlife Service foraging habitat thresholds, our analysis using LiDAR-derived habitat data indicated thresholds in fine-grained resource use by foraging RCWs on the Savannah River Site can be characterized by a range of conditions bounded with upper and lower breakpoints. Home-range analyses indicated neighboring RCWs maintained overlapping home ranges with nearly exclusive core areas across all density conditions. Home range overlap and frequency of neighboring group interactions tended to increase with neighboring group density and had negative effects on RCW group fitness. Fine-grained space use models included covariates for the number of neighboring groups within 200-m and LiDAR-derived habitat thresholds. Our results indicate RCWs dedicate more effort to territorial defense under high density conditions, potentially at the expense of greater foraging efficiency and time allocated to rearing young, as evidenced by reduced fitness. The positive spatial association between resource selection by foraging RCWs and distribution of neighboring groups indicates once a minimal set of structural habitat thresholds are reached, proximity to neighboring groups is a primary factor driving habitat use by foraging RCWs. We conclude that resource selection and space use by foraging RCWs is not solely determined by foraging habitat thresholds defined in the species' recovery plan, but also the distribution and distance to neighboring groups that operate at smaller scales. Additional consideration for the distribution and number of neighboring RCW groups will allow managers to prioritize areas for RCW conservation based on population density and habitat structure, both of which have important effects on RCW habitat use, but only one of which is integrated into current habitat management guidelines.

Population-density Mediated Resource Partitioning by Foraging Red-cockaded Woodpeckers

by
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A dissertation submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

Fisheries, Wildlife, and Conservation Biology

Raleigh, North Carolina
2017

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DEDICATION

I dedicate my dissertation to my family for their enduring support.

BIOGRAPHY

James Edward Garabedian was born in Columbia, Maryland, on March 9, 1986. After graduating from Archbishop Spalding High School in 2004, he pursued his Bachelor of Science degree in Environmental Biology at Wingate University, North Carolina, and graduated in 2008. He returned to Maryland after accepting a graduate teaching assistantship at Frostburg State University and graduated with a Master of Science degree in Applied Ecology and Conservation Biology in May 2010. Shortly after graduating from Frostburg State University, he was hired as a wildlife contractor to use non-lethal methods to mitigate wildlife hazards on United States military installations, but his passion for research brought him back to academia. In 2011, James accepted a research position with Dr. Christopher E. Moorman and Dr. M. Nils Peterson at North Carolina State University to study red-cockaded woodpecker foraging ecology. In 2013, James' research on red-cockaded foraging ecology resulted in the funding support for his dissertation research under the direction of Dr. Moorman and Dr. Peterson. James plans to continue along a path in ecological research as a postdoctoral scholar and later secure a position in academia.

ACKNOWLEDGMENTS

This research was made possible by funding from the U.S. Department of Energy, Savannah River Operations Office through the USDA Forest Service Savannah River (Interagency Agreement DE-AI09-00SR22188) under Cooperative Agreement #SRS 10-CS-11083601-003. I thank Dr. Christopher E. Moorman, Dr. Markus N. Peterson, Dr. John C. Kilgo, and Dr. Theodore R. Simons for guiding my research and writing efforts. Dr. Moorman, Dr. Peterson, and Dr. Kilgo played a central role in securing the funding for this project and provided valuable advice, constructive criticism, and encouragement throughout. Thank you for all your support and patience over the past four or so years! Dr. Simons added a valuable outside perspective to this work with many fruitful discussions and thought-provoking questions. Thank you for the fruitful and instructive discussions!

My dissertation has been improved by many colleagues and friends and I would like to thank everyone who has encouraged and supported me along the way. I am eternally grateful to my field crew - Mark Pavlosky, Jr., Aliza Sager, Dakotah Hunter, Chris Hansen, and Jessica Spickler. You guys will always be my A-team and I could not have asked for a better crew to work with! I especially thank Mark Pavlosky, Jr. for his unwavering dedication to this project and for being such a great colleague and friend. Thank you all so very much; you made this work possible – and much more fun!

Additionally, I would like to thank Tracy Grazia, Nancy Jordan, John Blake, Tal Mims, Jared Nance, and Anne Poole for facilitating site access, providing data, and for all the valuable discussions about woodpeckers along the way! I would also like to thank the USDA Forest Service-Savannah River staff for operational support and oversight for contract work involved with the acquisition of LiDAR data used in this study. I thank Sarah Slover for her vital assistance with graduate school requirements and deadlines – I cannot thank you enough for being my go-to person for administrative problems! Finally, I would like to thank Cynthia Burke for providing the best administrative support for my research!

I am especially grateful to my parents, Richard and Leanne Garabedian for all their support. I cannot thank you enough for your encouragement throughout this chapter in my life; I would not have been able to do it without you! I would like to express my deep gratitude to my sister, Mary George; no-one could ever have a better sister than you! I would also like to thank my brother-in-law Aaron George for letting me drink all your craft beer as I ramble on about woodpeckers!

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER 1: Use of LiDAR to Evaluate Alternative Habitat Thresholds for Conservation of an Endangered Woodpecker

CHAPTER 2: Space-use Sharing and Territoriality of an Endangered Woodpecker Across a Range of Local Density Conditions

CHAPTER 3: Modeling Fine-grained Resource Use to Inform Strategic Management of an Endangered Woodpecker

LIST OF FIGURES

CHAPTER 1: Use of LiDAR to Evaluate Alternative Habitat Thresholds for Conservation of an Endangered Woodpecker

CHAPTER 2: Space-use Sharing and Territoriality of an Endangered Woodpecker Across a Range of Local Density Conditions

CHAPTER 3: Modeling Fine-grained Resource Use to Inform Strategic Management of an Endangered Woodpecker

CHAPTER 1: Use of LiDAR to Evaluate Alternative Habitat Thresholds for Conservation of an Endangered Woodpecker

ABSTRACT

Quantifying species-habitat relationships provides guidance for establishment of recovery standards for endangered species, but research on woodland bird habitat has been limited by availability of fine-grained forest data across broad extents. New tools for collection of data on woodland bird response to fine-grained forest structure provide opportunities to evaluate habitat thresholds for woodland birds. We used LiDAR-derived estimates of habitat attributes and resource selection to evaluate foraging habitat thresholds for recovery of the federally endangered red-cockaded woodpecker (*Leuconotopicus borealis*; RCW) on the Savannah River Site, South Carolina. First, we generated utilization distributions to define habitat use and availability for 30 RCW groups surveyed over a 4-hour period twice per month between April 2013 and March 2015. Next, we used piecewise regression to characterize RCW threshold responses in use of LiDAR-derived habitat attributes described in the United States Fish and Wildlife Service recovery plan for RCW. Finally, we used resource utilization functions to estimate selection of specific habitat thresholds and used the magnitude of selection to prioritize thresholds for conservation strategies. We identified lower and upper thresholds for densities of pines $\geq$35.6 cm dbh (22, 65 trees/ha), basal area (BA) of pines $\geq$25.4 cm dbh (1.4, 2.2 m^2/ha), hardwood canopy cover (6, 31%), and BA of hardwoods 7.6-22.9 cm dbh (0.4, 6.07 m^2/ha); we identified three thresholds for density of pines 7.6-25.4 cm dbh (56, 341, and 401 trees/ha). Selection rankings prioritized foraging habitat with <6% hardwood canopy cover (β = 0.254, 95% CI = 0.172 – 0.336), <1.2 m^2/ha BA of hardwoods 7.6-22.9 cm dbh (β = 0.162, 95% CI = 0.050 – 0.275), >1.4 m^2/ha BA of pines $\geq$25.4 cm dbh (β = 0.055, 95% CI = 0.022 – 0.087), and $\geq$22 pines $\geq$35.6 cm dbh/ha (β = 0.015, 95% CI =

0.013 – 0.042). We identified habitat thresholds corresponding to open canopy structure, moderate densities of large and medium pines, and sparse hardwood midstory trees. Threshold selection ranks prioritized multiple thresholds below USFWS range-wide recovery thresholds, which indicates alternative management goals may be practical for site-specific RCW conservation compared to the range-wide guidelines. Based on our results, fine-grained LiDAR-derived habitat data coupled with GPS-derived habitat use can guide endangered species recovery by identifying the full range of structural conditions associated with threshold responses.

INTRODUCTION

Wildlife conservation has benefited from studies of animal habitat selection, particularly for endangered species. Studies of resource selection quantify species-habitat relationships and provide insight into key resources driving patterns in species' distribution, reproduction, and survival (Manly et al. 2007). The habitat conditions (e.g., vegetation composition or structure) where resource use is high relative to its availability offer empirical support for species' minimum habitat requirements and the resources critical for survival and reproduction (Rushton et al. 2004). Recovery of threatened and endangered species often relies on studies of resource selection in development of quantitative targets for protection of critical habitat (Hernández et al. 2006, Berl et al. 2015, Dinkins et al. 2016).

Resource selection functions (Manly et al. 2007) have benefited woodland bird conservation by identifying species-specific habitat thresholds where provision of habitat is a conservation priority (Berl et al. 2015). Species-habitat thresholds are defined as points or zones of nonlinear, abrupt change in species' response to relatively small changes in habitat conditions (Groffman et al. 2006). Habitat thresholds have been applied in a variety of contexts, including development of quantitative targets for species' minimum requirements related to forest stand structure (McKellar et al. 2014), patch connectivity (Knick et al. 2013, Taillie et al. 2015), and patch size (Collier et al. 2012, Dudley et al. 2012, Shake et al. 2012). These quantitative thresholds in turn serve as conservation targets to maximize species' productivity (Swift and Hannon 2010), increase availability of habitat (Camaclang et al. 2015), and identify areas with potential habitat that require targeted management to promote desired conditions (Suchant et al. 2003, Evans et al. 2014). Measuring and mapping habitat satisfying structural thresholds over broad areas allows managers to initiate specific management to promote desired habitat conditions (Martin et al. 2009). For example, conservation of brown creepers (*Certhia americana*) has relied on habitat thresholds to evaluate the potential impacts of timber harvest on minimum requirements in nesting habitat structure (Poulin et al. 2008, Poulin et al. 2010). Habitat thresholds have guided conservation of other woodland birds including Eurasian treecreepers (*C. familiaris*; Suorsa et al. 2005), white-browed treecreepers (*Climacteris affinis*; Radford and Bennett 2004), bachman's sparrows (*Peucaea aestivalis*; Allen and Burt 2014), olive-sided flycatchers (*Contopus cooperi*; Robertson 2012), and several woodpeckers (*Dendrocopus* spp., *Melanerpes* spp., *Picoides* spp., *Picus* spp.; Bütler et al. 2004, Roberge et al. 2008, Müller and Bütler 2010, Touihri et al. 2014, Berl et al. 2015)

There are practical challenges in deriving habitat thresholds for conservation of species that respond to fine-grain variation in forest structure (Müller and Bütler 2010, Berl et al. 2015). Ideally, spatial scales for research on species-habitat thresholds are based on species' ecology or conservation needs, but logistic difficulties in field data collection often result in a mismatch between scales of species response and habitat data (Johnson 1980, Wiens 1989, Boyce 2006, Meyer and Thuiller 2006, Gaillard et al. 2010). Coarse, stand-level forest inventory data may not capture the range of conditions that includes the true threshold, which can make threshold responses difficult to detect for specialist woodland birds (Marshall and Cooper 2004, Betts et al. 2007, Swift and Hannon 2010, Daily et al. 2012). Further, coarse measurements of forest structure collected at arbitrary extents can introduce bias in model estimates (Beyer et al. 2010, Kertson and Marzluff 2011, Northrup et al. 2013, Paton and Matthiopoulos 2016). Consequently, the mismatch between scales of habitat data and avian habitat selection behaviors has hampered identification of thresholds in species' response to forest structure and could mislead conservation efforts (Johnson et al. 2004, Betts et al. 2007, Bennett et al. 2013).

Advances in global positioning systems (GPS) and remote sensing technology offer new potential for research on the generality of threshold responses to forest structure by woodland birds (Ficetola et al. 2014). Light detection and ranging (LiDAR) can capture a range of ecologically meaningful forest structural attributes that can be mapped at fine-grains and broad extents (i.e., small units measured over a large area) as needed for species with complex structural habitat requirements (He et al. 2015). Wilsey et al. (2012) used LiDAR-derived habitat variables to evaluate alternative habitat suitability models for the endangered black-capped vireo (*Vireo atricapilla*) and reported LiDAR data improved their ability to identify current habitat while effectively differentiating potential habitat for improvement with targeted management. Additionally, researchers using LiDAR have identified new ranges of structural conditions associated with occupancy of woodland birds, including red-naped sapsuckers (*Sphyrapicus nuchalis*; Holbrook et al. 2015), black-throated blue warblers (*Setophaga caerulescens*; Goetz et al. 2010), and brown creepers (*Certhia americana*; Vogeler et al. 2013), that stimulated new perspectives on habitat thresholds for each species. Global positioning systems technology facilitated greater precision in linking habitat characteristics to individual bird locations for modeling species-habitat relationships at biologically meaningful spatial scales (Vierling et al. 2013, Vogeler et al. 2013, Ackers et al. 2015). Greater precision of bird locations may be particularly valuable for analysis of habitat thresholds for species that respond to fine-grained variability in forest structure or the presence/absence of discrete critical resources (e.g., nest cavities; Roberge et al. 2008, Anich et al. 2012).

Conservation of the federally endangered red-cockaded woodpecker (*Leuconotopicus borealis*; RCW) would benefit from research on structural thresholds that define foraging habitat quality (United States Fish and Wildlife Service [USFWS] 1970, 2003). Habitat loss, particularly longleaf pine (*Pinus palustris*) forests and old pines required for nesting and roosting, was the primary historic cause of the species' decline (Ligon et al. 1986, Conner and Rudolph 1989, Walters et al. 2002). As nesting constraints are now mitigated using techniques such as prescribed burning and artificial cavity construction (Copeyon 1990, Allen 1991), a better understanding of factors contributing to foraging habitat quality has gained importance in the recovery of this species (Walters et al. 2002, USFWS 2003). Foraging RCWs consistently exhibit a range-wide preference for the largest and oldest available pines (Porter and Labisky 1986, Engstrom and Sanders 1997, Zwicker and Walters 1999, Walters et al. 2002). Additionally, researchers have documented positive relationships between RCW group productivity and open foraging habitat with low to intermediate pine densities, some large and old pines, sparse hardwood midstory, and abundant herbaceous groundcover (James et al. 1997, 2001, Walters et al. 2002). Foraging habitat guidelines included in the species' recovery plan reflect these relationships and define quantitative targets for range-wide RCW conservation (USFWS 2003). Foraging habitat quality is evaluated based on the acreage of habitat satisfying threshold requirements of key structural attributes including: 1) $\geq$40% herbaceous groundcover; 2) sparse hardwood midstory that is <2.1 m in height; 3) basal area (BA) and density (stems/ha) of pines $\geq$35.6 cm dbh are $\geq$4.6 m^2/ha and $\geq$45 stems/ha, respectively; 4) BA of pines 25.4-35.6 cm dbh is $\leq$9.2 m^2/ha; 5) BA of pines $\geq$25.4 cm dbh is $\geq$2.3 m^2/ha; 6) BA and density of pines <25.4 cm dbh are $\leq$2.3 m^2/ha and $\leq$50 stems/ha, respectively; 7) <30% hardwood canopy cover; and 8) foraging habitat that satisfies all recommendations is not separated by >61 m (USFWS 2003). The foraging habitat guidelines also recommend all foraging habitat be within 0.8 km of the cluster (i.e., the aggregation of active and inactive cavity trees defended by a single RCW group; USFWS 2003), and that >50% be within 0.4 km of the cluster.

Although resource selection by foraging RCWs has been studied extensively, there has been little empirical support for the foraging habitat thresholds included in the USFWS recovery plan as quantitative targets for RCW conservation (Garabedian et al. 2014*b*). Spadgenske et al. (2005) reported acreage of foraging habitat in compliance with USFWS structural thresholds for recovery did not significantly influence RCW reproductive success in Georgia. Using LiDAR-derived habitat data from Savannah River Site, South Carolina, Garabedian et al. (2014*a*) estimated only ~31% of habitat within 800-m foraging partitions surrounding active clusters complied with any 4 of 6 USFWS range-wide threshold requirements, but demonstrated the potential for LiDAR to quantify habitat thresholds for RCW conservation. Using regression trees, McKellar et al. (2014) demonstrated thresholds in forest stand structure related to RCW reproductive success vary among populations across the species' range and concluded site-specific modifications of current USFWS foraging habitat thresholds could benefit RCW recovery.

In this study, we used high-resolution LiDAR-derived estimates of forest structure and GPS tracking data to determine whether foraging RCWs exhibit threshold responses in use of fine-grained forest structure and to evaluate empirical support for application of USFWS recovery guidelines for RCW conservation on Savannah River Site, South Carolina. Specifically, we: 1) used GPS locations of foraging RCWs collected throughout the year to estimate utilization distributions and define habitat availability and use for individual RCW groups; 2) estimated thresholds in habitat use by foraging RCWs relative to fine-grained LiDAR-derived structural estimates of forest attributes described in the USFWS foraging habitat guidelines; 3) modeled selection of LiDAR-derived foraging habitat that satisfied structural threshold requirements to rank and prioritize local conservation strategies; and 4) modeled relationships between RCW fledgling production and selection of structural habitat thresholds to determine if provision of specific thresholds influence RCW group fitness.

STUDY AREA

The Savannah River Site, an 80,267-ha National Environmental Research Park owned and operated by the U.S. Department of Energy, is located on the Upper Coastal Plain and Sandhills physiographic provinces in South Carolina, USA. The Savannah River Site is characterized by sandy soils and gently sloping hills dominated by pines with scattered hardwoods (Kilgo and Blake 2005). Prior to acquisition by the Department of Energy in 1951, the majority of the Savannah River Site was maintained in agricultural fields or recently was harvested for timber (White 2005). The U.S. Department of Agriculture Forest Service has managed the natural resources of the Savannah River Site since 1952 and reforested >90% of the site (Imm and McLeod 2005, White 2005). Approximately 53,014 ha of the Savannah River Site has been reforested with artificially regenerated stands of loblolly (*P. taeda*), longleaf (*P. palustris*), and slash (*P. elliottii*) pines with an additional 2,832 ha with pine-hardwood mixtures (Imm and McLeod 2005). The remaining ~20% of the forested area includes bottomland hardwoods, forested swamps/riparian areas, and mixed-hardwood stands (Imm and McLeod 2005).

In conjunction with the Department of Energy, the Forest Service began management and research on the RCW in 1984 with the objective to restore a viable population on the

Savannah River Site. Under intensive management since 1985, the RCW population had grown from 3 active clusters with 5 birds (Johnston 2005) to 91 active clusters with more than 250 birds in 2016 (T. Mims, *pers. comm.*). The Savannah River Site RCW population is designated as a secondary core population in the South Atlantic Coastal Plain recovery unit and must support >250 potential breeding groups (i.e., a male and female occupying the same cluster of cavity trees) at the time of and after delisting (USFWS 2003). All RCWs at the Savannah River Site are uniquely color-banded by Forest Service personnel as part of ongoing monitoring.

METHODS

Woodpecker demographic data. The Forest Service conducted RCW group observations and nest checks during each nesting season since 1985 to determine clutch size, nestling production, fledgling production, and group size for each RCW group. Of the 67 active clusters at the Savannah River Site in 2013 (Figure 1.1), we selected a sample of 30 that minimally consisted of a male and female (i.e., a potential breeding group) between 2009 and 2013. Reproductive success metrics represented means of annual observations for fledgling production and group size for each of the 30 sample groups. We included group size because larger RCW groups tend to have greater reproductive success (Walters 1990, Khan and Walters 2002). Fledgling production data were averaged using observations from 2009-2013. Group size data were averaged using observations from 2010-2013 because data from 2009 were unavailable.

Home-range surveys. We followed the sample of 30 foraging RCW groups minimally over a 4-hour period, using handheld GPS to record locations at 15-min intervals (Franzreb 2006), twice a month between April 2013 and March 2015. Minimally, we recorded 15 location fixes throughout the day during each follow, thus providing ≥30 relocations per month. Follows consisted of sustained visual contact with individuals of the sample group beginning when individuals left their roosts in the morning and continuing until contact with the birds was lost, or until terminated due to inclement weather or management activities that precluded site access (e.g., prescribed burning). Although RCW group members tend to forage near one another, even concurrently in the same tree (Franzreb 2006), we used location fixes for the breeding male of each sample group to represent movement of the entire group. We considered follows incomplete if we recorded <15 location fixes throughout a single day and repeated incomplete follows at a later date of the same month. In addition to location fixes, observers documented basic behaviors (e.g., foraging, resting, cavity work, feeding nestlings, or interspecific interaction) at each 15-min interval. Because our analysis focused on resource selection by foraging RCWs, we used only foraging relocations in subsequent analyses.

LiDAR-derived habitat data. We used high-resolution LiDAR-derived estimates of forest structure to quantify foraging habitat available to individual RCW groups. We acquired high density (mean of 10 returns m^{-2}) airborne LiDAR across the Savannah River Site during leaf-off conditions in February and March 2009. We used circular, fixed-area plots to collect field vegetation data on 194 ground calibration plots located throughout Savannah River Site across a range of forest conditions in the spring of 2009. On each plot, we measured forest attributes included in the USFWS range-wide foraging habitat guidelines, including BA and density of pine trees that were ≥35.6, 25.4–35.6, and 7.6–25.4 cm dbh, and hardwoods that were 7.6–22.9 and ≥22.9 cm dbh.

Next, we used regression methods to relate LiDAR sensor data to forest inventory attributes measured on ground calibration plots. We used the best subsets approach to select the set of LiDAR explanatory variables based on model fit and residual standard error for each forest structure response variable. We used the variance inflation factor statistic to eliminate highly collinear predictor variables (Fox and Monette 1992). If variance inflation factor exceeded 5.0 for a candidate predictor variable, we dropped it from the regression model.

We used several modeling steps to estimate LiDAR-derived structural habitat attributes. First, we used nonlinear seemingly unrelated regression to develop models for BA and density of hardwood, softwood, and all plot trees ≥7.6 cm dbh. This additive regression approach ensured hardwood and softwood regression model estimates for each ground calibration plot summed to the regression model estimate for all plot trees (Parresol 2001). We then applied the nonlinear seemingly unrelated regression approach to the explanatory variables and their coefficients from these regression models as initial values in a system of three equations (one for hardwood, one for softwood, and one for all plot trees).

Next, we developed multiple linear regressions to estimate specific RCW habitat attributes. We used the same model selection and evaluation methods as described in the nonlinear seemingly unrelated regression approach (i.e., model fit, residual standard error, and variance inflation factor). To estimate variables bounded by a lower dbh limit (e.g., BA of pines ≥25.4 cm dbh), we developed an independent multiple regression model for each variable using only trees measured on ground calibration plots that were above the specified dbh limit as the response. We estimated variables bounded by an upper and lower dbh limit (e.g., BA of pines 7.6–25.4 cm dbh) by subtracting estimates of two regressions. We developed one regression using only trees larger than the lower dbh limit and a second model using only trees larger than the upper dbh limit. We computed the predictions for both the upper and lower dbh limit regressions across the entire LiDAR acquisition area at 20-m resolution using ArcGIS Spatial Analyst Raster Calculator (ESRI 2011). We subtracted the raster layer containing predictions of the second regression model (upper dbh limit) from the predictions of the first (lower dbh limit) to produce an estimate for trees with dbh between the upper and lower dbh limit. We then used the regression models to populate raster layers with estimates of forest structure at 20-m resolution for all of the Savannah River Site.

Finally, we quantified the error in model predictions over several square aggregate sizes (i.e., grain size) to determine the size that reduced prediction error while still maintaining a biologically meaningful grain size. Based on prediction error, we selected 0.64 ha, or 80x80-m grid cells, as the grain size for our analyses (Garabedian et al. 2014*a*). Additional details of the analytical approach used to model forest structure using LiDAR data on the Savannah River Site are provided by Garabedian et al. (2014*a*).

Utilization distributions. We used fixed-kernel density methods and the reference bandwidth to estimate utilization distributions (UD; Worton 1989) from RCW group foraging locations. These UDs defined habitat availability and probability of use for individual RCW sample groups. Utilization distributions define space use as a continuous and probabilistic process throughout the home range that can be visualized as a gridded three-dimensional surface representing the relative probability of use at specific locations (Millspaugh et al. 2006). The advantages of UDs over other methods to quantify resource use by foraging RCWs is that use is not treated as a dichotomous response (i.e., used or unused; Millspaugh et al. 2006) and the approach objectively defines the extent of available habitat

(Kertson and Marzluff 2011). Using separate UDs for all tracked individuals, rather than their individual relocations, treats individual RCW groups as independent sampling units and mitigates confounding effects related to spatial autocorrelation of relocations (Aebischer et al. 1993, Otis and White 1999). Another advantage of smoothing functions is flexibility to control the spatial resolution of the grid on which we estimated RCW UDs without the need to change the UD surface itself (Calenge 2011). In other words, we could specify the resolution of all RCW UDs to match the 0.64-ha resolution of the LiDAR-derived habitat data without major changes to UD heights or shape of the surface (Marzluff et al. 2004, Calenge 2011). We analyzed RCW locations and estimated UDs in the R statistical environment (R Development Core Team 2015) using the contributed packages “sp” (Pebesma and Bivand 2005, Bivand et al. 2013) and “adehabitatHR” (Calenge 2006).

Threshold analysis. We used piecewise regression to model threshold responses in resource use by foraging RCWs in response to LiDAR-derived estimates of forest structure (Muggeo 2003, Toms and Lesperance 2003). Piecewise regression is a breakpoint-based technique to identify abrupt changes in species’ response relative to the variable(s) of interest (Toms and Villard 2015). Additionally, we extended piecewise regressions to account for the possibility of multiple breakpoints, such as upper and lower bounds on structural habitat conditions, which could provide a more realistic approach to defining structural habitat thresholds for conservation (Ficetola and Denoël 2009).

We fit piecewise regressions using UD-volume as the response variable and mean values of individual LiDAR-derived habitat attributes as predictors. We used 50 bootstrap samples to estimate standard errors for piecewise regressions fitting 1, 2, and 3 breakpoints. We used Akaike’s Information Criterion (AIC; Akaike 1974) to compare regression models and select the most parsimonious model (Burnham and Anderson 2002). In the case of multiple competing threshold models (e.g., ΔAIC <2.0 for models with 1 and 2 breakpoints), we compared models by overlaying model breakpoints and bootstrapped standard errors on the distribution of UD-volumes and mean values of individual LiDAR-derived habitat attributes (e.g., Homan et al. 2004). We selected the final model with fitted lines and breakpoint estimates that best fit the distribution of the raw data.

We used the breakpoints identified in the most parsimonious piecewise regression model to define alternative RCW habitat thresholds for use in subsequent analyses. We used slope estimates of individual fitted segments from each of the most parsimonious piecewise regression models to determine how the threshold should be applied on the landscape (e.g., positive and negative slopes representative of minimum requirements and maximum tolerance, respectively). For example, a positive slope for use of habitat with ≥45 large pines/ha would represent a minimum requirement for large pines/ha; a negative slope associated with ≥45 large pines/ha would represent a maximum tolerance. We fit piecewise regression models in the R statistical environment (R Development Core Team 2015) using the contributed package "segmented" (Muggeo 2008).

Resource utilization functions. We developed spatially-explicit resource utilization functions (RUFs; Marzluff et al. 2004) to quantify selection of LiDAR-derived foraging habitat satisfying three different sets of habitat thresholds, including: 1) USFWS range-wide structural thresholds for RCW recovery; 2) lower piecewise regression breakpoints; and 3) upper piecewise regression breakpoints. For each set of habitat thresholds, we fit RUFs for each sample RCW group using 99% UD volumes and dummy variables indicating whether the 0.64-ha pixel satisfied the structural threshold requirements (identified in the USFWS foraging habitat guidelines or breakpoints identified by piecewise regressions) as the response and predictors, respectively. Within 99% UD-volume contours for each RCW group, we enumerated 0.64-ha pixels that satisfied: 1) structural threshold requirements of good quality foraging habitat described in the current USFWS foraging habitat guidelines; 2) forest structure associated with lower breakpoints in use identified using piecewise regression; and 3) forest structure associated with upper breakpoints in use identified using piecewise regression. Because individual-level RUF coefficients are considered independent replicated measures, they can be used to estimate population-wide utilization values (Marzluff et al. 2004). Additionally, standardized RUF coefficients can be used to rank the importance of foraging habitat attributes based on relative magnitude and direction of coefficients. Standardized RUF coefficients >0 indicate the foraging habitat attribute is used more relative to availability; coefficients <0 indicate use is lower relative to availability.

We fit RUFs using Matern correlation functions, which are flexible and can capture effects of spatial autocorrelation among adjacent sample units across a range of conditions, including the spatial autocorrelation between the probability of use among adjacent UD pixels (Marzluff et al. 2004). Matern correlation functions are estimated in RUFs using maximum-likelihood techniques and require initial values for two parameters: 1) the range of spatial dependence, measured in meters; and 2) the smoothness of the UD surface, measured in derivatives of the UD surface. For our analysis, we follow recommendations of Marzluff et al. (2004) and set initial values for the range of spatial dependence as the bandwidth for each RCW group UD and set the smoothness of each UD surface to 1.5. We used the R statistical environment and the contributed package “ruf” for analysis and development of RUFs (R Development Core Team 2015, Handcock 2015).

Modeling reproductive success. The independence among RUF coefficients for individual RCW groups enabled their use as explanatory variables in subsequent analyses (Aebischer et al. 1993). The relative magnitude of resource selection as characterized by individual-group RUF coefficients may provide a better metric to describe relationships between foraging habitat structure and RCW reproductive success compared to the number of acres satisfying structural threshold values (e.g., Spadgenske et al. 2005). In this case, the sample size becomes the number of sampled RCW groups, and RUF coefficients for each foraging habitat attribute represent independent replicated measures of selection. Thus, we used multiple linear regression to relate standardized RUF coefficients of individual RCW groups to mean fledgling production between 2009 and 2013. We included group size as an additional predictor to account for potential benefits to RCW reproduction (Khan and Walters 2002). We used second-order biased Akaike's Information Criterion (AIC_c; Hurvich and Tsai 1989) to rank fitted multiple linear regression models and select the most parsimonious model (Burnham and Anderson 2002).

RESULTS

Woodpecker data. Overall means of reproductive success metrics at the Savannah River Site were within the range of those reported in previous studies (Table 1.1). We documented over 17,000 locations for 30 neighboring RCW groups between April 2013 and March 2015. These included approximately 15,000 foraging relocations, and the remaining 2,000 relocations represented ancillary behaviors such as resting, incubation, or cavity maintenance. The reference bandwidths (i.e., smoothing parameters) estimated for individual RCW group UDs averaged 83 m and ranged from 46-126 m. The total area available to

RCWs within boundaries of 99% UD volume contours averaged 135 ha and ranged from 48-304 ha.

Threshold analysis. The most parsimonious piecewise regressions identified breakpoints in use at lower and upper values for density of pines $\geq$35.6 cm dbh (22, 65 trees/ha), BA of pines $\geq$25.4 cm dbh (1.4, 2.2 m^2/ha), hardwood canopy cover (6, 31%), and BA of hardwoods 7.6-22.9 cm dbh (0.4, 6.07 m^2/ha); breakpoints were identified at three values for density of pines 7.6-25.4 cm dbh (56, 341, and 401 pines/ha; Table 1.2). Habitat use by foraging RCWs relative to density of pines $\geq$35.6 cm dbh/ha increased up to approximately 22 pines/ha, did not significantly change between 22 and 65 pines/ha, and decreased beyond 65 pines/ha (Table 1.3). Habitat use relative to BA of pines $\geq$25.4 cm dbh/ha increased up to approximately 1.4 m^2/ha, increased at a lower rate between 1.4 and 2.2 m^2/ha, and decreased beyond 2.2 m^2/ha (Table 1.3). Habitat use relative to density of pines 7.6-25.4 cm dbh/ha increased up to approximately 56 pines/ha, increased at a lower rate between 56 and 341 pines/ha, decreased between 341 and 400 pines/ha, and continued to decrease beyond 400 pines/ha (Table 1.3). Habitat use relative to BA of hardwoods 7.6-22.9 cm dbh/ha decreased up to approximately 0.4 m^2/ha, decreased at a lower rate between 0.4 and 6.7 m^2/ha, and continued to decrease beyond 6.7 m^2/ha (Table 1.3). Habitat use relative to hardwood canopy cover/ha decreased up to 6% cover, decreased at a lower rate between 6% and 31%, and continued to decrease beyond 31% (Table 1.3). Overall, the range of structural conditions represented by lower and upper breakpoints in habitat use identified by piecewise regression included range-wide structural thresholds in the USFWS recovery plan (Table 1.4; Figures 1.2-1.6).

Resource utilization functions. Selection of foraging habitat varied between USFWS thresholds and piecewise regression breakpoints, but some general patterns in selection emerged for specific foraging habitat attributes (Table 1.5). Overall, we detected selection of habitat related to thresholds in density of pines $\geq$35.6 cm dbh/ha, BA of pines $\geq$25.4 cm dbh, BA of hardwoods 7.6-22.9 cm dbh, and percent hardwood canopy cover (Table 1.5). The magnitude of selection and ranked importance of each habitat attribute varied among models (Table 1.5). In the USFWS threshold model, selection was ranked highest for habitat with <1.2 m^2/ha BA of hardwoods 7.6-22.9 cm dbh, followed by selection for habitat with $\geq$2.3 m^2/ha BA of pines $\geq$25.4 cm dbh, and selection for habitat with <30% hardwood canopy cover (Table 1.5). In the models based on lower piecewise regression breakpoints, selection was ranked highest for habitat with <6% hardwood canopy cover, followed by selection for habitat with <0.4 m^2/ha BA of hardwoods 7.6-22.9 cm dbh, selection for habitat with $\geq$1.4 m^2/ha BA of pines $\geq$25.4 cm dbh, and selection for habitat with $\geq$22 pines $\geq$35.6 cm dbh/ha (Table 1.5). In the models based on upper piecewise regression breakpoints, we did not detect selection or avoidance of habitat satisfying threshold requirements (Table 1.5).

Modeling reproductive success. The most parsimonious regression model of RCW fledgling production was fit with selection coefficients for upper piecewise regression breakpoints and group size (Table 1.6). The regression model accounted for approximately 43% of the variation in fledgling production ($F_{6,22} = 4.471$, $p = 0.004$). Selection of habitat with $\leq$65 pines $\geq$35.6 cm dbh/ha and RCW group size had significant negative and positive effects on fledgling production, respectively (Table 1.6). There was moderate agreement between observed fledgling production in 2015 and that predicted by the fitted regression model for 5-year mean fledgling production (Figure 1.7).

DISCUSSION

Our findings suggest RCW conservation may benefit from replacing the fixed range-wide structural thresholds of foraging habitat quality with site-specific intervals defined by breakpoints. In contrast to range-wide USFWS recovery thresholds, thresholds in resource use by foraging RCWs on Savannah River Site can be characterized by a range of conditions bounded with upper and lower breakpoints. Our analysis supports previous studies of RCW habitat selection across the species' range that describe good quality foraging habitat as having a low basal area and open canopy, low to moderate densities of medium and large pines, and minimal hardwood encroachment (James et al. 1997, 2001, Walters et al. 2002); however, the structural threshold requirements in the USFWS recovery plan appeared too strict to account for the range of habitat conditions used throughout the year by foraging RCWs on Savannah River Site. Habitat thresholds that define a range of structural conditions with upper and lower bounds can be used to develop more flexible guidelines for RCW conservation.

Defining thresholds based on selection of LiDAR-derived habitat data and effects on RCW group fitness provided insight into potential consequences for management for conditions above or below threshold requirements. We provide empirical support for previous assertions that the benefits of large pines are diminished at higher tree densities (e.g., Walters et al. 2002, McKellar et al. 2014), which is particularly important for RCW conservation given the priority to retain the largest and oldest pines across the landscape. While we advocate maintenance of the largest and oldest pines in RCW foraging habitat, under current conditions on Savannah River Site, the range-wide USFWS target of ≥45 pines ≥35.6 cm dbh/ha had slightly negative effects on resource selection by foraging RCWs. In contrast, selection of habitat satisfying the lower piecewise regression breakpoint of ≥22 pines ≥35.6 cm dbh suggests reducing the minimum requirement for large pines would provide a more appropriate target to maintain open canopy structure and moderate stocking densities that are associated with increased RCW productivity (e.g., James et al. 1997, 2001, Walters et al. 2002). In Florida, Hardesty et al. (1997) reported inverse relationships between RCW group reproduction and BA of pines >30.5 cm dbh and density of all pines >25.4 cm dbh/ha within group home ranges, suggesting canopy closure due to increased pine densities, including large pines, can decrease habitat quality and reproduction. Natural pruning could occur at greater rates in dense pine stands, which can limit prevalence of large dead branches that support high arthropod biomass in RCW foraging habitat (Smith 1955, Hooper 1996). Additionally, high stand densities could decrease levels of calcium and nitrogen in the soil, which in turn may indirectly limit nutritive value of RCW arthropod prey (Taylor 1986, Graveland and Van Gijzen 1994, James et al. 1997, Palik et al. 1997). Recent studies reported a higher threshold for pines ≥35.6 cm dbh/ha could be adopted on many other sites but would require site-specific adjustments (McKellar et al. 2014). Based on our results, Savannah River Site would require site-specific adjustments that lower the threshold requirement for density of pines ≥35.6 cm dbh from ≥45 to ≥22 pines/ha.

Our results indicate a threshold for all pines ≥25.4 cm dbh may be a more robust standard of foraging habitat quality for RCWs than mutually exclusive thresholds for pines ≥35.6 and ≥25.4 cm dbh and would provide greater transferability to sites across the species' range. Our results are consistent with selection for all pines ≥25.4 cm dbh on Savannah River

Site reported in previous research (Franzreb 2006) as well as other studies on RCW resource selection. McKellar et al. (2015) combined metrics for density of pines 25.4-35.6 cm dbh/ha and pines ≥35.6 cm dbh/ha in Florida because there were not enough pines ≥35 cm dbh on the landscape in Florida to fit each metric separately. Hooper and Harlow (1986) reported some evidence for selection of stands relative to density of pines ≥25.4, ≥35.6, and ≥48 cm dbh, but overall there was no indication for increased stand selection for pine size classes above ≥25.4 cm dbh. DeLotelle et al. (1983) reported stand selection by foraging RCWs in central Florida increased relative to density of pines ≥10 cm dbh when pines ≥30 cm dbh were rare on the landscape. Zwicker and Walters (1999) reported differential use of pines ≥35.6 cm dbh in North Carolina, but overall trends indicated use only began to exceed availability for trees ≥25.4 cm dbh.

Defining habitat use as a continuous rather than dichotomous process may explain the differences in thresholds prioritized by our models compared to previous studies. Our UD-based approach treated all pixels within UDs of individual RCW groups as available, thus we had greater power to parse variation in intensity of use across the range of habitat conditions available to individual groups (Kertson and Marzluff 2011). For example, foraging RCWs appeared to be sensitive to hardwood canopy cover and midstory encroachment at fine grains, even at levels below the USFWS range-wide threshold requirements. These results contrast recent range-wide research that suggested ongoing management has reduced hardwood midstory encroachment to the point it has limited negative effects on RCW reproductive success or foraging habitat quality (McKellar et al. 2014, 2015). However, our results suggest minimizing hardwood midstory and canopy trees in RCW foraging habitat remains a priority on Savannah River Site due to potential impacts on resource use at finer scales. In east Texas, Macey et al. (2016) identified a significant threshold for hardwood midstory basal area (~0.36 m^2/ha) comparable to what we identified in South Carolina (~0.4 m^2/ha), indicating fine-grained thresholds for hardwood midstory encroachment remain a priority on other sites as well. Although frequent fire in RCW foraging habitat has minimized hardwood midstory encroachment, it has not eliminated hardwood midstory trees from RCW foraging habitat on Savannah River Site. Moderate patches of hardwood midstory trees in RCW foraging habitat, although scattered, still impede movement among trees by foraging RCWs and thus could limit foraging efficacy and food intake (Blancher and Robertson 1987, Daan et al. 1988, Jackson and Parris 1995).

Previous efforts to validate RCW foraging habitat models suggest poor model generalization could be remedied by including additional habitat data from more sites (e.g., McKellar et al. 2014), but our results suggest social information and a metric for group size may be more beneficial than additional structural habitat data. Although the independent observations of RCW fledgling production generally aligned with the fitted line from the multiple linear regression model, the width of prediction confidence intervals indicate the structural habitat thresholds in our models still did not capture important processes driving variation in RCW reproduction. Group size was related to RCW group reproduction, likely due to the contribution of helpers to RCW reproductive success (Khan and Walters 2002). Additionally, population viability models for RCWs highlight the importance of including social information and consequences for reproductive success when using these models to guide management (Zeigler and Walters 2014).

MANAGEMENT RECOMMENDATIONS

Development of RCW foraging habitat guidelines based on a range of structural conditions will allow managers to consider new areas as RCW foraging habitat and provide the flexibility to prioritize targets for specific forest attributes. Greater flexibility to manage new areas as RCW foraging habitat can be achieved on the Savannah River Site by: 1) reducing the minimum threshold requirements for pines $\geq$35.6 cm dbh from $\geq$45 pines/ha to $\geq$22 pines/ha, while continuing to protect the largest and oldest pines in RCW foraging habitat; 2) reducing the minimum requirements for BA of pines $\geq$25.4 cm dbh to $\geq$1.4 m^2/ha; 3) maintaining hardwood midstory BA below 1.2 m^2/ha, ideally using prescribed fire to gain potential indirect benefits of herbaceous understory on RCW foraging habitat quality (James et al. 1997, 2001); and 4) increasing the maximum threshold for pines $<$25.4 cm dbh from $<$50 to $<$400 pines/ha. Additionally, greater flexibility can be achieved by simplifying mutually exclusive criteria for pines $\geq$35.6 and $\geq$25.4 cm dbh into a single metric describing densities of all pines $\geq$25.4 cm dbh until pines $\geq$35.6 cm dbh are more abundant across the landscape. Based on ranked magnitude of selection by foraging RCWs, we recommend managers prioritize availability of foraging habitat with: 1) BA of pines $\geq$25.4 cm dbh $\geq$1.4 m^2/ha; 2) hardwood midstory BA $<$1.2 m^2/ha; 3) $\geq$22 pines $\geq$35.6 cm dbh/ha; and 4) $<$400 pines $<$25.4 cm dbh/ha.

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Table 1.1 Average clutch size, nestling production, fledgling production, and group size averages and variation reported from previous research across the range of the red-cockaded woodpecker.

Source	Location	Clutch	Nestling	Fledgling	Group
This Study	Savannah River Site	2.9 (0.1)	1.8 (0.1)	1.4 (0.1)	2.4 (0.1)
Butler and Tappe 2008	AR and LA	3.2 (0.4)	2.1 (0.4)	1.5 (0.4)	2.4 (0.2)
Engstrom and Sanders 1997	The Wade Tract (1993/1994)	3.3/3.6	2.5/2.5	2.5/2.3	3/3.6
Hooper and Lennartz 1995	Francis Marion NF	2.7 (0.23)	1.7 (0.24)	1.2 (0.16)	2.4 (0.17)
James et al. 1997	Apalachicola NF	3.3 (0.9)		1.4 (0.7)	2.4 (0.6)
James et al. 2001	Apalachicola NF				
	Wakulla District			0.67 (0.5)	1.6 (0.8)
	Apalachicola District			1.1 (0.4)	2.2 (0.2)
Wigely et al. 1999	Louisiana	3.3 (0.1)		1.4 (0.1)	2.3 (0.005)
Spadgenske et al. 2004	Fort Stewart	2.7 (0.1)		1.6 (0.1)	2.5 (0.06)

Table 1.2. Comparison of piecewise regression models estimating 1, 2, and 3 breakpoints in habitat use by foraging red-cockaded woodpecker groups (*n* = 30) relative to LiDAR-derived estimates of structural attributes included in the United States Fish and Wildlife Service foraging habitat guidelines on the Savannah River Site, South Carolina, between April 2013 and March 2015.

LiDAR-derived habitat attribute	AIC	ΔAIC	*n* breakpoints	Breakpoint estimates
Pines ≥35.6 cm dbh/ha	128116.4	0.0	2	22.0, 64.9
	128118.4	2.0	3	23.6, 73.0, 95.2
	128119.7	3.3	1	45.9
	128164.7	48.3	0	
Pines 7.6-25.4 cm dbh/ha	127920.4	0.0	3	56.8, 341.8, 401.9
	127946.5	26.1	2	55.9, 218.1
	127956.9	36.5	1	152.8
	128159.9	239.5	0	
BA (m^2/ha) of pines ≥25.4 cm dbh	127979.5	0.0	2	1.4, 2.2
	127982.9	3.4	3	1.4, 2.5, 5.7
	127985.2	5.7	1	2.1
	128155.8	176.3	0	
BA hardwoods 7.6-22.9 cm dbh	127483.6	0.0	2	0.4, 6.1
	127484.5	0.9	3	0.2, 1.7, 5.5
	127487.5	3.9	1	0.4
	127638.8	155.2	0	
Hardwood canopy cover	127413.9	0.0	2	6.4, 31.5
	127433.3	19.4	3	0.2, 6.1, 32.6
	127439.1	25.2	1	8.6
	127596.6	182.7	0	

[a] Models with 0 breakpoints were simple linear regression models that did not estimate thresholds.

Table 1.3. Top piecewise regression models selected from candidate models estimating 1, 2, and 3 breakpoints in habitat use by foraging red-cockaded woodpecker groups (n = 30) relative to LiDAR-derived estimates of structural attributes defined in the United States Fish and Wildlife Service foraging habitat guidelines on the Savannah River Site, South Carolina, between April 2013 and March 2015.

Piecewise regression	Intercept	Slope (SE)	95% CI
Pines ≥35.6 cm dbh/ha			
$x < 22$	6.626	0.194 (0.061)	0.073 – 0.314
$22 < x < 65$	11.180	0.001 (0.017)	-0.033 – 0.034
$x > 65$	22.550	-0.174 (0.037)	-0.247 – -0.102
BA (m^2/ha) pines ≥25.4 cm dbh/ha			
$x < 1.4$	0.064	7.727 (1.097)	5.577 – 9.878
$1.4 < x < 2.2$	8.219	2.068 (0.953)	0.200 – 3.936
$x > 2.2$	20.650	-3.179 (0.518)	-4.194 – -2.164
Pines 7.6-25.4 cm dbh/ha			
$x > 56$	4.051	0.117 (0.024)	0.071 – 0.163
$56 < x < 341$	10.180	0.01 (0.003)	0.005 – 0.016
$341 < x < 400$	49.060	-0.103 (0.042)	-0.186 – -0.021
$x > 400$	9.084	-0.003 (0.003)	-0.008 – 0.002
BA (m^2/ha) hardwoods 7.6-22.9 cm dbh/ha			
$x < 0.4$	17.170	-14.02 (2.067)	-18.08 – -9.973
$0.4 < x < 6.1$	11.760	-1.341 (0.164)	-1.662 – -1.02
$x > 6.1$	6.957	-0.441 (0.267)	-0.965 – 0.083
Hardwood canopy cover/ha (%)			
$x < 6$	18.700	-1.245 (0.14)	-1.520 – -0.970
$6 < x < 31$	12.290	-0.245 (0.032)	-0.307 – -0.183
$x > 31$	5.758	-0.049 (0.051)	-0.148 – 0.050

Table 1.4. Definition of LiDAR-derived structural thresholds defined by the United States Fish and Wildlife Service (USFWS) foraging habitat guidelines, lower piecewise regression breakpoints in habitat use by foraging red-cockaded woodpecker groups, and upper piecewise regression breakpoints in habitat use by foraging red-cockaded woodpecker groups (n = 30) on the Savannah River Site, South Carolina, between April 2013 and March 2015.

LiDAR-derived habitat attribute	Variable description
USFWS foraging habitat thresholds	
Pines ≥35.6 cm dbh/ha	Ha of foraging habitat with ≥45 pines/ha that are ≥35.6 cm dbh
Pines 7.6-25.4 cm dbh/ha	Ha of foraging habitat with <50 pines/ha that are 7.6-25.4 cm dbh
BA of pines ≥25.4 cm dbh	Ha of foraging habitat with BA ≥2.3 m^2/ha of pines ≥25.4 cm dbh
Hardwood canopy cover	Ha of foraging habitat with <30% hardwood canopy cover
BA hardwoods 7.6-22.9 cm dbh	Ha of foraging habitat with BA <1.2 m^2/ha of hardwoods 7.6-22.9 cm dbh
Lower piecewise regression thresholds	
Pines ≥35.6 cm dbh/ha	Ha of foraging habitat with ≥22 pines/ha that are ≥35.6 cm dbh
Pines 7.6-25.4 cm dbh/ha	Ha of foraging habitat with ≥56 pines/ha that are 7.6-25.4 cm dbh
BA of pines ≥25.4 cm dbh	Ha of foraging habitat with BA ≥1.4 m^2/ha of pines ≥25.4 cm dbh
Hardwood canopy cover	Ha of foraging habitat with <6% hardwood canopy cover
BA hardwoods 7.6-22.9 cm dbh	Ha of foraging habitat with BA <0.4 m^2/ha of hardwoods 7.6-22.9 cm dbh
Upper piecewise regression thresholds	
Pines ≥35.6 cm dbh/ha	Ha of foraging habitat with <65 pines/ha that are ≥35.6 cm dbh
Pines 7.6-25.4 cm dbh/ha	Ha of foraging habitat with <401 pines/ha that are 7.6-25.4 cm dbh
BA of pines ≥25.4 cm dbh	Ha of foraging habitat with BA <2.2 m^2/ha of pines ≥25.4 cm dbh
Hardwood canopy cover	Ha of foraging habitat with <31% hardwood canopy cover
BA hardwoods 7.6-22.9 cm dbh	Ha of foraging habitat with BA <6.1 m^2/ha of hardwoods 7.6-22.9 cm dbh

Table 1.5. Standardized resource utilization functions, including mean selection (Mean β), 95% confidence intervals, and proportion of RCW groups (*n* = 30) with positive/negative selection estimates (Direction) in response to LiDAR-derived habitat thresholds. Thresholds were defined by United States Fish and Wildlife Service (USFWS) foraging habitat guidelines, lower piecewise regression breakpoints in habitat use by foraging red-cockaded woodpecker groups, and upper piecewise regression breakpoints in habitat use by foraging red-cockaded woodpecker groups on the Savannah River Site, South Carolina, between April 2013 and March 2015.

Variables[a]	Mean β	95% CI	Direction	
			+	-
USFWS thresholds				
≥45 pines ≥35.6 cm dbh/ha	-0.110	-0.273, 0.053	20	10
<50 pines 7.6-25.4 cm dbh/ha	-0.039	-0.102, 0.023	13	17
≥2.3 m^2/ha BA of pines ≥25.4 cm dbh*	0.178	0.016, 0.339	15	15
<1.2 m^2/ha BA of hardwoods 7.6-22.9 cm dbh*	0.263	0.166, 0.359	24	6
<30% hardwood canopy cover/ha*	0.106	0.037, 0.176	16	14
Lower piecewise regression thresholds				
≥22 pines >35.6 cm dbh/ha*	0.029	0.013, 0.042	18	12
≥56 pines 7.6-25.4 cm dbh/ha	0.014	-0.238, 0.262	16	14
≥1.4 m^2/ha BA of pines >25.4 cm dbh*	0.081	0.012, 0.247	19	11
<0.4 m^2/ha BA of hardwoods 7.6-22.9 cm dbh*	0.158	0.050, 0.275	24	6
<6% hardwood canopy cover/ha*	0.254	0.172, 0.336	19	11
Upper piecewise regression thresholds				
<65 pines ≥35.6 cm dbh/ha	-0.021	-0.201, 0.159	17	13
<401 pines 7.6-24.5 cm dbh/ha	0.014	-0.122, 0.150	16	14
<2.2 m^2/ha BA of pines ≥25.4 cm dbh	-0.025	-0.367, 0.316	14	16
<6.1 m^2/ha BA of hardwoods 7.6-22.9 cm dbh	-0.106	-0.225, 0.013	9	21
<34% hardwood canopy cover/ha	-0.085	-0.203, 0.033	11	19

[a] Variables with 95% confidence intervals that did not overlap 0 were considered statistically significant effects at alpha=0.05 and are denoted by asterisks.

Table 1.6. Multiple linear regression models with coefficients (β) and standard errors (SE) relating red-cockaded woodpecker group (n = 30) fledgling production to selection of LiDAR-derived structural thresholds. Thresholds were defined by United States Fish and Wildlife Service (USFWS) foraging habitat guidelines, lower piecewise regression breakpoints in habitat use by foraging red-cockaded woodpecker groups, and upper piecewise regression breakpoints in habitat use by foraging red-cockaded woodpecker groups on the Savannah River Site, South Carolina, between April 2013 and March 2015. Parameters with significant effects are denoted by asterisks.

Model	Parameter	AIC_c	β	SE	t-value	Pr (>|t|)
USFWS thresholds		51.8				
	Pines ≥35.6 cm dbh/ha		-0.429	0.358	-0.224	0.825
	BA (m^2/ha) of pines ≥25.4 cm dbh		0.030	0.308	0.990	0.922
	Pines 7.6-25.4 cm dbh/ha		-0.113	0.300	-0.337	0.709
	BA hardwoods 7.6-22.9 cm dbh		0.123	0.229	0.537	0.596
	Hardwood canopy cover		-0.589	0.327	-1.804	0.084
	Group size*		0.592	0.204	2.897	0.008
Lower piecewise regression thresholds		52.3				
	Pines ≥35.6 cm dbh/ha		-0.814	0.482	-1.690	0.104
	BA of pines ≥25.4 cm dbh		-0.444	0.421	-1.054	0.302
	Pines 7.6-25.4 cm dbh/ha		0.076	0.295	0.258	0.798
	BA hardwoods 7.6-22.9 cm dbh		-0.228	0.219	-1.041	0.308
	Hardwood canopy cover		0.074	0.211	0.351	0.728
	Group size*		0.638	0.194	3.285	0.003
Upper piecewise regression thresholds		42.6				
	Pines ≥35.6 cm dbh/ha*		-1.274	0.403	-3.163	0.004
	BA of pines ≥25.4 cm dbh		0.248	0.282	0.881	0.387
	Pines 7.6-25.4 cm dbh/ha		-0.537	0.365	-1.472	0.155
	BA hardwoods 7.6-22.9 cm dbh		0.424	0.402	1.054	0.303
	Hardwood canopy cover		0.671	0.388	1.728	0.097
	Group size*		0.466	0.167	2.800	0.010

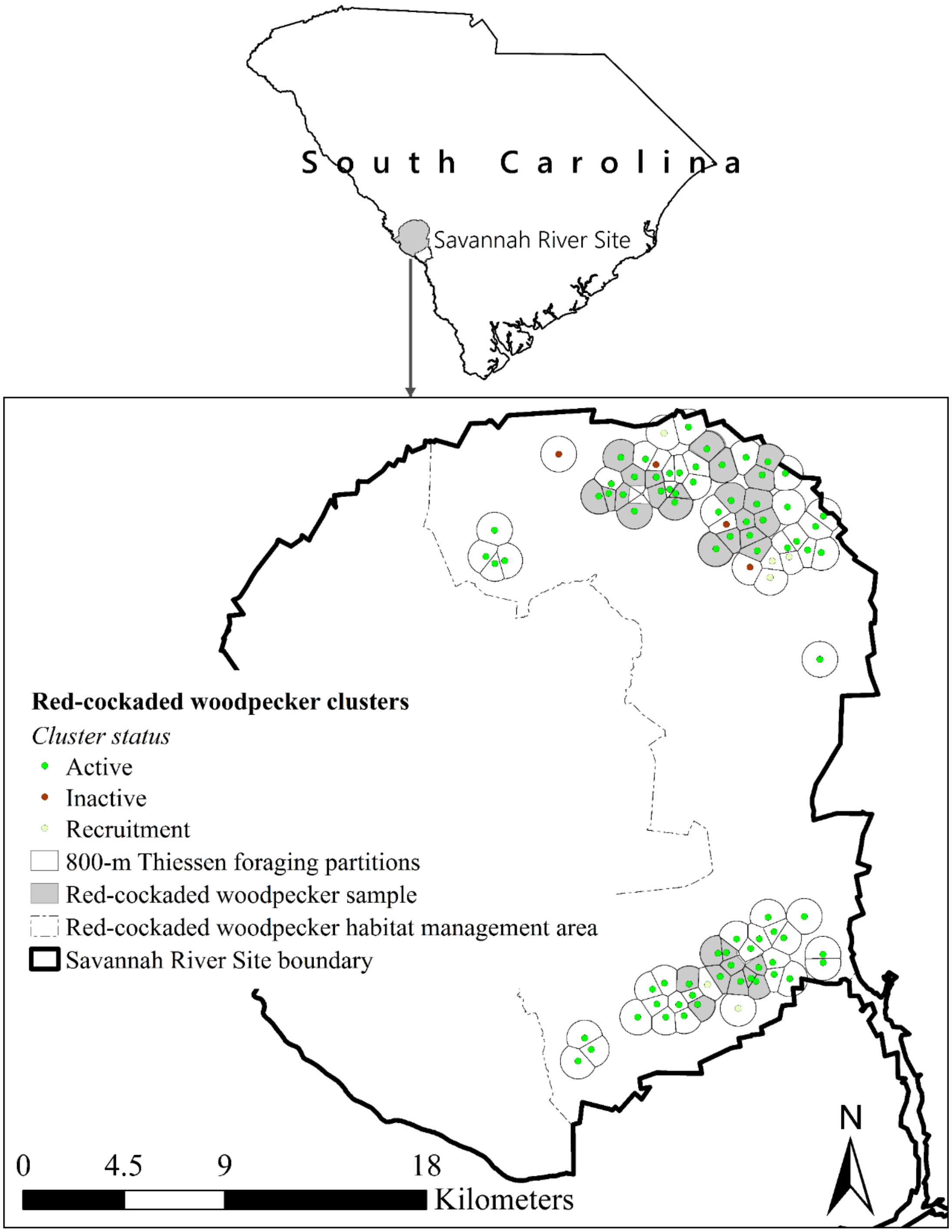

Figure 1.1 The spatial distribution and status of red-cockaded woodpecker cavity tree clusters on Savannah River Site, South Carolina, in 2013.

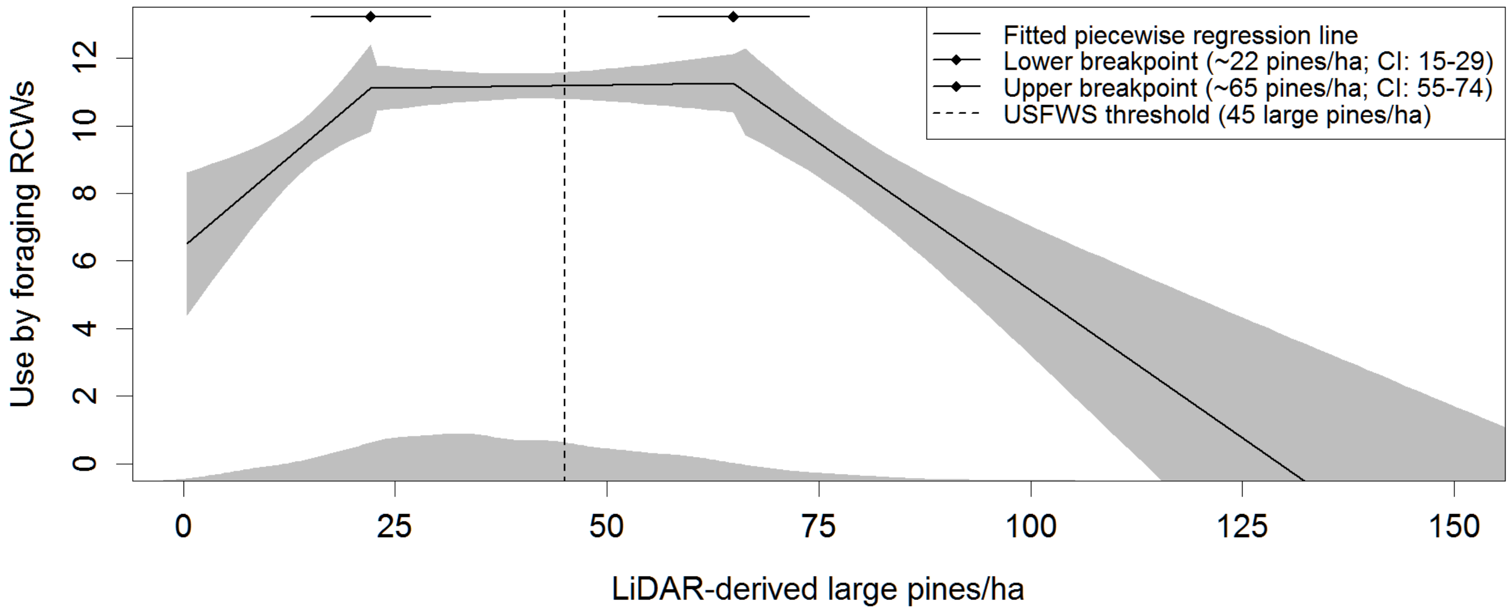

Figure 1.2. Fitted piecewise regression model, breakpoints, and 95% confidence intervals (shaded area around fitted line) in resource use by foraging red-cockaded woodpecker groups (*n* = 30) relative to LiDAR-derived density of pines $\geq$35.6 cm dbh/ha on Savannah River Site, South Carolina, between April 2013 and March 2015. Shaded areas along the x-axis represent the smoothed distribution of density values at 0.64-ha grains within 99% utilization distribution volume contours of all sampled woodpecker groups.

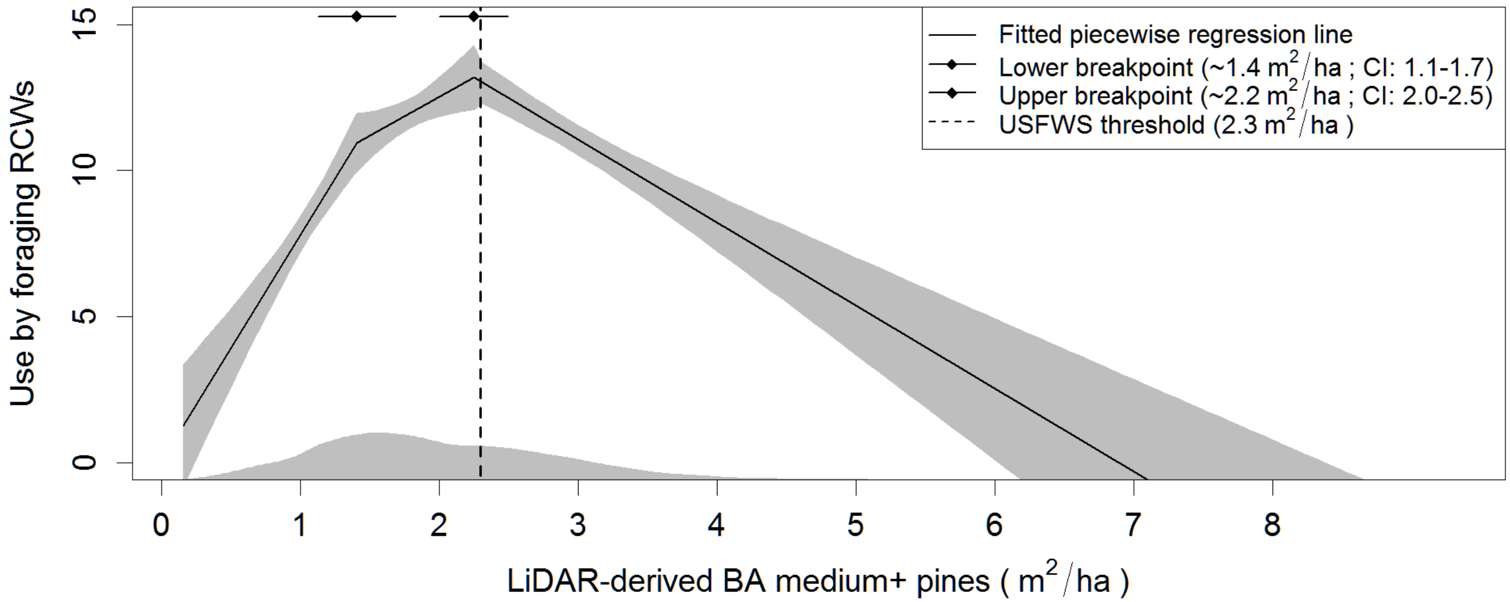

Figure 1.3. Fitted piecewise regression model, breakpoints, and 95% confidence intervals (shaded area around fitted line) in resource use by foraging red-cockaded woodpecker groups (*n* = 30) relative to LiDAR-derived basal area (BA; m^2/ha) of pines $\geq$25.4 cm dbh on Savannah River Site, South Carolina, between April 2013 and March 2015. Shaded areas along the x-axis represent the smoothed distribution of BA values at 0.64-ha grains within 99% utilization distribution volume contours of all sampled woodpecker groups.

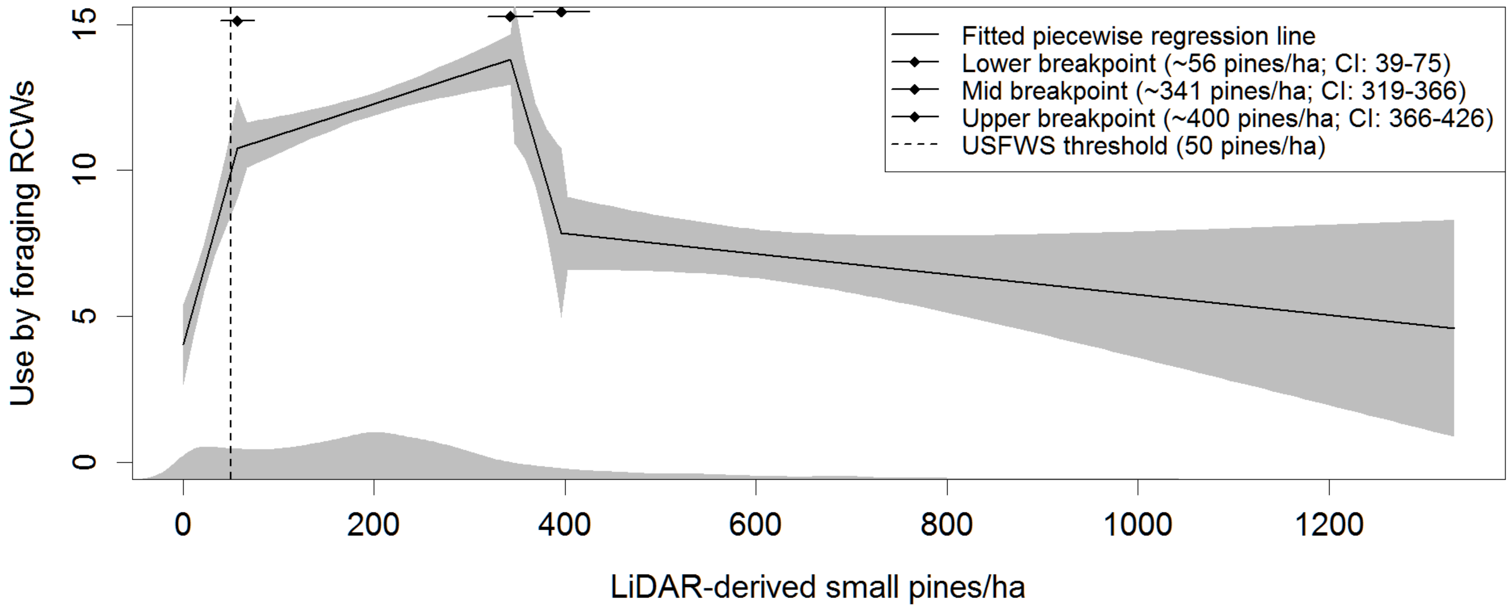

Figure 1.4. Fitted piecewise regression model, breakpoints, and 95% confidence intervals (shaded area around fitted line) in resource use by foraging red-cockaded woodpecker groups (*n* = 30) relative to LiDAR-derived density of pines 7.6-25.4 cm dbh/ha on Savannah River Site, South Carolina, between April 2013 and March 2015. Shaded areas along the x-axis represent the smoothed distribution of density values at 0.64-ha grains within 99% utilization distribution volume contours of all sampled woodpecker groups.

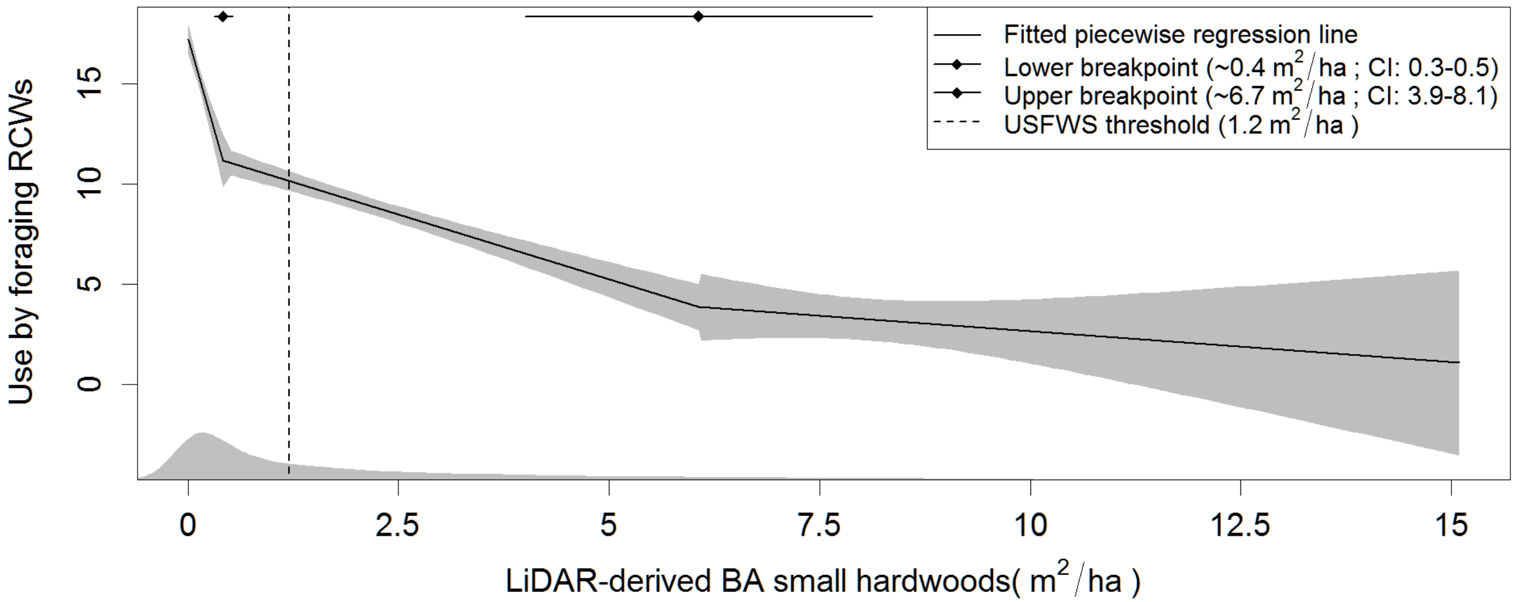

Figure 1.5. Fitted piecewise regression model, breakpoints, and 95% confidence intervals (shaded area around fitted line) in resource use by foraging red-cockaded woodpecker groups (*n* = 30) relative to LiDAR-derived basal area (BA; m^2/ha) of hardwoods 7.6-22.9 cm dbh on Savannah River Site, South Carolina, between April 2013 and March 2015. Shaded areas along the x-axis represent the smoothed distribution of BA values at 0.64-ha grains within 99% utilization distribution volume contours of all sampled woodpecker groups.

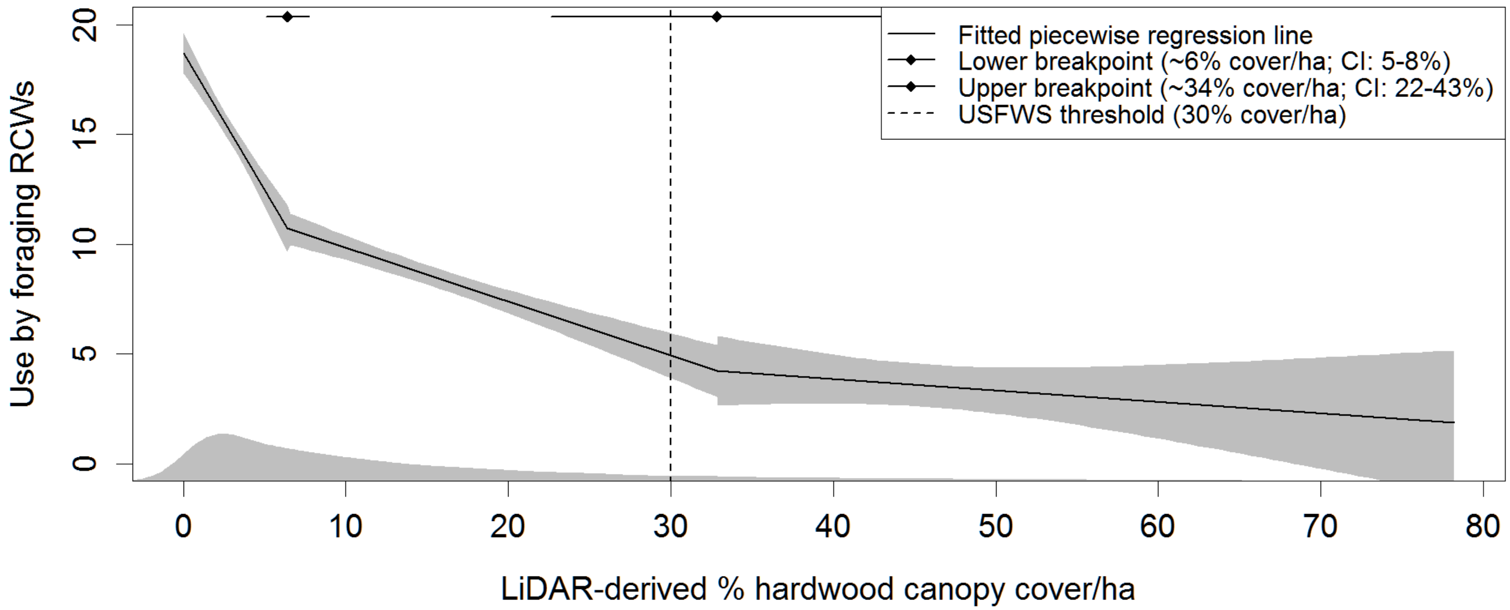

Figure 1.6. Fitted piecewise regression model, breakpoints, and 95% confidence intervals (shaded area around fitted line) in resource use by foraging red-cockaded woodpecker groups (*n* = 30) by foraging RCWs relative to LiDAR-derived percent hardwood canopy cover on Savannah River Site, South Carolina, between April 2013 and March 2015. Shaded areas along the x-axis represent the smoothed distribution of percent canopy cover values at 0.64-ha grains within 99% utilization distribution volume contours of all sampled woodpecker groups.

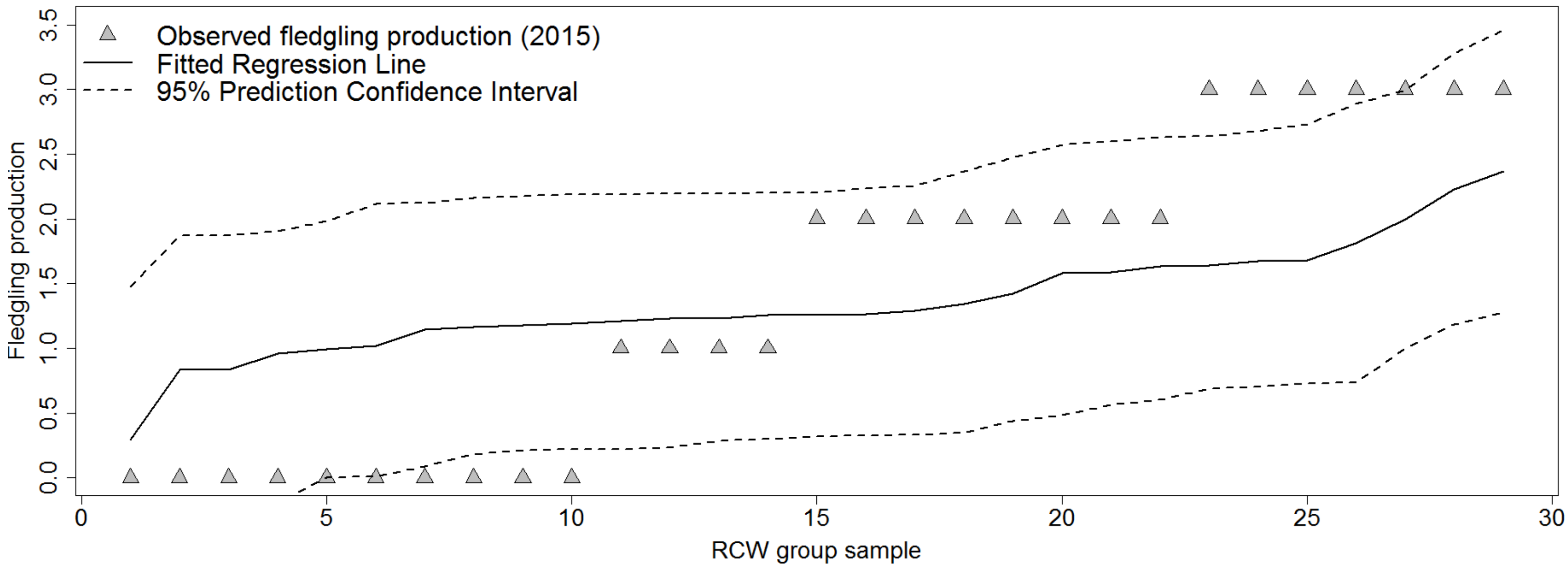

Figure 1.7. Prediction confidence intervals for multiple linear regression modeling 5-year mean (2009-2013) fledgling production in response to selection of LiDAR-derived habitat thresholds and group size for red-cockaded woodpecker groups (n = 30) on Savannah River Site, South Carolina. Habitat thresholds were defined by upper piecewise regression breakpoints in habitat use by foraging red-cockaded woodpecker groups on Savannah River Site between April 2013 and March 2015. Grey triangles represent observations of fledgling production by the same sample of 30 woodpecker groups in 2015.

CHAPTER 2: Space-use Sharing and Territoriality of an Endangered Woodpecker Across a Range of Local Density Conditions

ABSTRACT

Home range and territory characteristics (e.g., size, spatial overlap) may vary in response to conspecific density, in turn influencing the effectiveness of conservation strategies. We used the endangered red-cockaded woodpecker (*Leuconotopicus borealis*; RCW) as a case study to investigate the effects of conspecific density on home range characteristics. We used home range data to determine whether neighboring RCW groups shared foraging habitat at the same levels across a range of density conditions or whether groups instead reduced their home range size as density increased, and we investigated how changes in response to density may influence group reproductive success on two sites in South Carolina, USA. We documented over 36,000 locations from 44 groups of RCWs in three density condition classes between April 2013 and March 2015. The frequency of neighboring group interactions differed among density conditions and was greatest for high-density groups. RCW home ranges and core areas were larger under low-density conditions ($\bar{x}_{\text{Home range}}$ = 88.4 ha, $\bar{x}_{\text{Core area}}$ = 21.0 ha) than under medium ($\bar{x}_{\text{Home range}}$ = 68.29 ha, $\bar{x}_{\text{Core area}}$ = 16.6 ha) and high-density ($\bar{x}_{\text{Home range}}$ = 76.3 ha, $\bar{x}_{\text{Core area}}$ = 18.6 ha) conditions. Neighboring RCWs maintained overlapping home ranges with nearly exclusive core areas across all density conditions, but overlap tended to increase with greater neighboring group density. Under high-density conditions, home range overlap had negative effects on clutch size (β = -0.19, SE = 0.09), nestling production (β = -0.37, SE = 0.09), and fledgling production (β = -0.34, SE = 0.0.08). Our results indicate RCWs dedicate more effort to territorial defense under high density conditions, potentially at the expense of greater foraging efficiency and time allocated to rearing young, as evidenced by reduced fitness. High home range overlap

indicated the absence of territoriality farther away from nesting and roosting cavities, but exclusive core areas suggest RCW groups are territorial and defend habitat closer to the cavity tree cluster. Thiessen foraging partitions used to allocate foraging habitat will provide comprehensive habitat protection, but managers should be aware they may overestimate the extent of core areas defended by individual RCW groups and do not account for overlapping home ranges that can reduce RCW group fitness.

INTRODUCTION

Knowledge of home range and territory characteristics offers practical guidance for conservation of territorial resident birds with limited habitat (Adams 2001). Estimates of home range size are valuable for conservation efforts, such as reserve design (Schoener 1968, Villarreal et al. 2014, Hartmann et al. 2017) and determining minimum area requirements for endangered species recovery (Hernández et al. 2006, Smith et al. 2016, Kolts and McRae 2017). Home range shapes can be used to guide local management strategies, such as identifying locations for food supplementation (López-López et al. 2014), selecting sites for habitat restoration (Luck 2002, Bennett et al. 2012, 2013, Stanton et al. 2015), and determining compliance with regulatory guidelines for endangered species recovery (Fedy et al. 2014, Garabedian et al. 2014*a*). Intraspecific competition can influence the configuration of home ranges or territories (Krebs 1971, Adams 2001, Kokko and Lundberg 2001), which in turn may influence accessibility of limited resources (Pasinelli et al. 2001). Home range overlap and effects on fitness can be important to identify spacing requirements that minimize competition and optimize species' productivity (Mänd et al. 2009, Kašová et al. 2014, Sharps et al. 2015, Tao et al. 2016).

Home ranges, like territories, are economical in that birds routinely adapt them in response to individual condition (e.g., age, reproductive status), available food resources, nest sites, or conspecific density (Andrewartha and Birch 1954, Ford 1983, Smith and Shugart 1987, Adams 2001, Both and Visser 2003). Home range and territory sizes generally share an inverse relationship with food availability (Hixon 1980, Cody 1985). Home range and territory characteristics also depend on the density of conspecifics that compete for available resources (Brown 1964, Hixon 1980). A large home range or territory that includes abundant food may lead to higher fitness, but it also may attract conspecifics to the area and increase competition (Brown 1969, López-Sepulcre and Kokko 2005). Birds may respond to increases in conspecific density and competition by reducing the size of home ranges and territories, but there likely is a minimum size required to supply the resources needed for survival and reproduction (Nice 1941, Enoksson and Nilsson 1983, Both et al. 2000). Alternatively, birds may respond to increases in conspecific density by defending only the intensively used area around the nest site (Brown and Orians 1970, Both and Visser 2003, Poulin et al. 2010, Bauder et al. 2016, Fernández-Bellon et al. 2016). Defense of smaller intensively used areas within larger home ranges that overlap with neighboring conspecifics may be common in territorial birds (Potts 2014). Even during the breeding season, home ranges of territorial birds can extend beyond the defended territory (Anich et al. 2008, Streby et al. 2012).

Home range overlap has been associated with increases in conspecific density in many species, but how resident territorial birds partition use of overlapping areas is not well understood (Stamps 1990, Mclouglin et al. 2000, Elchuk et al. 2003). Avoidance of overlapping areas could be a mechanism to reduce the frequency of agonistic interactions (Moorcroft and Lewis 2006). Some territorial birds tolerate overlap with conspecifics in areas with abundant resources, but avoid defended areas surrounding neighboring nest sites (Goldenberg et al. 2016). Other birds maintain high home range overlap but avoid direct interaction with neighboring conspecifics through temporal partitioning (Anich et al. 2009). Increases in home range overlap can directly affect fitness of territorial resident birds, but limited research has explored these relationships (Both 1998, Newton 1998, López-Sepulcre et al. 2009).

Behavioral observations can provide further insight on the interplay between conspecific density and space-use overlap in resident birds that maintain all-purpose territories throughout the year (Newton 1992, Both and Visser 2003, Krüger et al. 2012, Grünkorn et al. 2014, Schuppe et al. 2016). Home range overlap suggests resources or space are partitioned to some degree, which can increase the frequency of competitive interactions (Ims 1987, Stamps 1990). Crowding effects and increased intraspecific competition under high population densities could require birds to dedicate more time to territorial defense at the expense of nestling provisioning (Sillett et al. 2004, Bretagnolle et al. 2008). Reduced foraging rates at higher levels of competition lead to higher mortality in adults (Stillman et al. 2000) and nestlings (Fielding 2004). Additionally, territorial interactions between neighboring conspecifics may spatially restrict foraging areas and exacerbate seasonal food limitations by preventing expansion of home range or territory boundaries (Fernandez et al. 2012).

Variation in red-cockaded woodpecker (*Leuconotopicus borealis*; RCW) space-use overlap and territorial behaviors in response to conspecific density may have important implications for applicability of standardized Thiessen foraging partitions for delineation of critical habitat across the species' range, as currently recommended by the U.S. Fish and Wildlife Service Recovery Plan for the species (U.S. Fish and Wildlife Service [USFWS] 2003). The RCW is an endangered territorial resident bird endemic to southern pine (*Pinus* spp.) forests of the United States (USFWS 1970, 2003). The most appropriate method to delineate foraging habitat to individual RCW groups is using home range data (USFWS 2003). However, this method requires extensive time and resources and rarely is used as a result (Convery and Walters 2004). Alternatively, the USFWS recommends use of Thiessen polygons to create mutually exclusive foraging partitions that delineate an area around each cavity tree cluster such that the partition boundaries equally divide space between all neighboring RCW groups (hereafter, Thiessen partitions; Lipscomb and Williams 1996).

Although standard Thiessen partitions provide a reasonable method to delineate RCW foraging habitat, considerable variation in RCW home range sizes raises uncertainty in whether this method accurately represents home range or territory characteristics under variable density conditions (Garabedian et al. 2014*a*). Current research indicates RCWs maintain large home ranges and defend large year-round territories ranging 50-150 ha that can vary extensively with population density (Hooper et al. 1982, Davenport et al. 2000, Conner et al. 2001, Pasinelli and Walters 2002, McKellar et al. 2015). Additionally, relatively high densities and small home ranges can occur on what is perceived as excellent (Wade Tract; Engstrom and Sanders 1997) as well as poor (Savannah River Site in early-1990's; Franzreb 2006) quality habitat, suggesting RCW home range dynamics and effects on group fitness are driven in part by factors other than foraging habitat quality. Red-cockaded woodpeckers are known to exhibit stronger territoriality in proximity of the cavity tree cluster (i.e., the aggregation of cavity trees used by members of a single group; Ligon 1970, Lennartz et al. 1987), but whether territorial defense extends to the entire home range, particularly that reflected in Thiessen partitions, is uncertain. Delotelle et al. (1987) reported 94% of RCW territorial interactions occurred within defended territory boundaries but were not observed in certain parts of home ranges that overlapped with neighboring groups. Although some studies suggest overlapping home ranges may have limited impact on fitness (Engstrom and Sanders 1997), others indicate it can limit reproductive success (DeLotelle and Epting 1992).

RCWs are an ideal focal species for determining how resident territorial species adjust behaviors to balance range sharing and territoriality as population density increases, and how these adjustments may influence group reproductive success. Because the application of Thiessen partitions for habitat delineation assumes neighboring RCWs partition space into discrete territories with no overlap (Nilsen et al. 2007, Schlicht et al. 2014), reports of overlapping home ranges suggest the method could be flawed when applied to high density populations. We investigated RCW home range dynamics across a gradient of neighboring group density conditions. Specifically, our objectives were to: 1) investigate space-use sharing and territoriality by foraging RCWs across a gradient of local neighboring group density conditions; 2) determine whether home range dynamics change with neighboring group density and if those changes influence RCW group fitness; and 3) evaluate concordance between USFWS foraging partitions and RCW space-use estimates in the context of space-use sharing and territorial behaviors.

METHODS

Study Sites

The Savannah River Site, an 80,267-ha National Environmental Research Park owned and operated by the U.S. Department of Energy, is located on the Upper Coastal Plain and Sandhills physiographic provinces in South Carolina, USA. The Savannah River Site is characterized by sandy soils and gently sloping hills dominated by pines with scattered hardwoods (Kilgo and Blake 2005). Prior to acquisition by the Department of Energy in 1951, the majority of the Savannah River Site was maintained in agricultural fields or recently had been harvested for timber (White 2005). The U.S. Department of Agriculture Forest Service has managed the natural resources of the Savannah River Site since 1952 and reforested the majority of the site (Imm and McLeod 2005, White 2005). Approximately

53,014 ha of the Savannah River Site is now reforested with artificially regenerated stands of loblolly (*P. taeda*), longleaf (*P. palustris*), and slash (*P. elliottii*) pines with an additional 2,832 ha with pine-hardwood mixtures (Imm and McLeod 2005). The remaining 27,000 ha of forested area on the Savannah River Site consists of bottomland hardwoods, forested swamps/streams, and mixed-hardwood stands (Imm and McLeod 2005). Under intensive management since 1985, the RCW population has grown from three groups of four birds (Johnston 2005) to 91 active groups of more than 250 birds in 2016 (T. Mims, *pers. comm.*).

The Carolina Sandhills National Wildlife Refuge, one of 14 Land Management and Research Demonstration areas managed by the USFWS, is located on the Atlantic Coastal Plain and Piedmont Plateau physiographic provinces, South Carolina, USA. The Carolina Sandhills National Wildlife Refuge is characterized by sandy soils dominated by upland, xeric pine woodlands. The refuge was established in 1939 from federal efforts to acquire eroded and abused lands from landowners that were provided with alternative, more productive lands elsewhere (USFWS 2010). The primary objectives of the refuge are: 1) to restore, maintain, and enhance longleaf pine habitat and associated plant and animal species; 2) to conserve, restore, and enhance threatened or endangered species, with special emphasis on the RCW; 3) to provide habitat for migratory birds; 4) to provide opportunities for environmental education, interpretation, and wildlife-oriented recreation; and 5) to demonstrate sound land management practices that enhance natural resource conservation (USFWS 2010). The refuge is approximately 19,364 ha, including 14,164 ha of predominantly longleaf pine-turkey oak (*P. palustris-Quercus cerris*) cover (USFWS 2010). The refuge harbors 150 active RCW clusters, representing the largest RCW population on USFWS lands. As part of ongoing monitoring efforts, Carolina Sandhills National Wildlife

Refuge personnel monitor nests and band nestlings with aluminum bands and unique combinations of color bands.

Data Collection

RCW sample selection.—We collected home-range data for 44 RCW groups between April 2013 and March 2015 (Figure 2.1). Individual RCW clusters were considered for sample selection if they had: 1) been active with a potential breeding group minimally for the past two years; and 2) not been identified as a captured cluster (a cluster that does not support its own group of RCWs, but contains active cavity trees) since 2011. We selected these criteria to increase the likelihood that clusters remained active with a potential breeding group throughout the duration of the study. We mapped clusters that satisfied these two primary selection criteria using geographic information systems to visually examine the spatial configuration of potential sample clusters (ESRI 2014). Individual clusters that satisfied the primary selection criteria were grouped into various 10-cluster aggregates for which the only selection criterion was that all clusters formed a spatially continuous aggregate (i.e., clusters within an aggregate did not all have to be within a certain distance, but must have formed a cohesive group).

We calculated neighboring group density as the number of groups per 50 ha of foraging habitat delineated by Thiessen partitions for RCWs within 10-cluster aggregates; we selected 50 ha to approximate the recommended minimum amount of good quality foraging habitat allocated to individual clusters (49 ha; USFWS 2003). Based on previous research, we considered ranges of 0.10–0.50, 0.51–1.00, and >1.00 groups/50 ha to represent low, medium, and high neighboring group density conditions, respectively. Researchers have suggested 1 RCW group/50 ha represents a “high” density population (Hooper and Lennartz

1995), 1 group/128 ha (or 0.39 groups/50 ha) represents a “moderate” density population (Conner et al. 1999), and 1 group/212 ha (0.23 groups/50 ha) represents a “low” density population (Conner et al. 1999). Neighboring group density estimates for low, medium, and high-density conditions in 2013 were approximately 0.42 groups/50 ha (Savannah River Site), 0.60 groups/50 ha (Savannah River Site), and 0.85 groups/50 ha (Carolina Sandhills National Wildlife Refuge), respectively. Neighboring group density estimates for low, medium, and high-density conditions in 2014 were approximately 0.39 groups/50 ha (Savannah River Site), 0.57 groups/50 ha (Savannah River Site), and 0.85 groups/50 ha (Carolina Sandhills National Wildlife Refuge), respectively. In 2014, we sampled an additional 10 groups under high neighboring group density conditions on Savannah River Site; estimated neighboring group density for this sample was approximately 0.77 groups/50 ha.

Home-range surveys.—We followed foraging RCW groups minimally over a 4-hour period, recording location fixes at 15-min intervals (Franzreb 2006), twice a month between March 2013 and April 2015. Minimally, we recorded 15 location fixes throughout the day during each follow, thus providing >30 relocations per month. In addition to location fixes, we documented basic behaviors (e.g., foraging, resting, cavity work, feeding nestlings, or interspecific interaction) at each 15-min interval. Survey efforts within each month were divided into two sampling periods during which we followed each sample RCW group once; we randomized sampling order within each period. During follows, we maintained visual contact with individuals of the sample group beginning when individuals left their roosts in the morning and continuing until contact with the birds was lost, or until terminated due to inclement weather or management activities that precluded site access (e.g., prescribed burning). We considered follows incomplete if <15 location fixes were recorded throughout a single day and repeated incomplete follows at a later date of the same month.

RCW group members tend to forage in close proximity to one another, even concurrently in the same tree (Franzreb 2006), so we used location fixes for the breeding male of each sample group to represent movement of the entire group. We adopted this approach for tracking RCW groups because breeding males are the most stable individual of the group, maintaining their breeding status until they die, and breeding males tend to be the dominant individual within the social hierarchy of each group (Conner et al. 2001). We used spotting scopes to re-sight and confirm unique color band combinations to ensure the breeding male was followed throughout the day.

Space-use estimation.—We used kernel density methods to estimate utilization distributions (UDs; Worton 1989) for each RCW sample group. Utilization distributions define space use as a continuous and probabilistic process throughout a predefined area and can be visualized as a three-dimensional surface reflecting the probability of habitat use at specific locations within that area (Millspaugh et al. 2006). Utilization distributions are well suited for experimental designs in which *n* unique individuals are sampled with the goal to describe home range and territory characteristics at the population or individual level (Millspaugh et al. 2006). We defined the home range and core areas as the 95% and 50% UD isopleths (Garrott and White 1990). We estimated seasonal and annual UD sizes and spatial overlap for sample RCW groups in each of low, medium, and high neighboring group density conditions. We quantified spatial overlap using the volume of intersection, or the cumulative sum of the minimum volume of intersection between corresponding pixels of overlapping areas of UDs (Fieberg and Kochanny 2005). Analysis of RCW relocations and generation of

UDs was conducted in the R statistical environment (R Development Core Team 2015) using the contributed packages “sp” (Pebesma and Bivand 2005, Bivand et al. 2013) and “adehabitatHR” (Calenge 2006).

Space-use analysis.—We used a chi-square test of proportions to characterize RCW home range behaviors in two ways. First, we determined whether 800-m Thiessen foraging partitions accurately reflected RCW habitat use by comparing the proportion of RCW locations within 800-m Thiessen partitions to the proportion outside partitions. Second, we investigated density-dependent changes in territorial behaviors by comparing the frequency of neighboring group interactions among density conditions.

We used a mixed-effects analysis of variance to compare home range and core area size and overlap estimates among low, medium, and high neighboring group density conditions. Fixed-effects included density condition, season, and year; individual group ID was fit as a random effect. We used mixed-effects multiple linear regression models to quantify relationships between RCW reproductive success and space use. We fit mean clutch sizes, nestling production, and fledgling production between 2009 and 2013 as the response variable. Because fledgling production was not independent between home-range and core-use area extents, we developed separate models relating fledgling production to size and overlap estimates from each extent. In each fitness model, we fit density condition, UD area estimates, UD spatial overlap, the interaction between density condition and UD area, and interaction between density condition and UD spatial overlap as predictors; group ID was fit as a random effect. Mixed-effects models were fit in the R statistical environment (R Development Core Team 2015) using the contributed package “lme4” (Bates et al. 2015).

RESULTS

We documented over 36,000 RCW locations between April 2013 and March 2015 (Table 2.1). Foraging and interspecific interactions were the most frequent and infrequent observations of RCWs, respectively, across all density conditions (Table 2.1). Frequency of neighboring group interactions differed among density conditions and was greatest among high-density groups (χ^2=179.26, *df*=27, *p*<0.001). Approximately 98% of foraging locations were within the total area of 800-m Thiessen partitions for 10-group clusters, but relocations often resulted in home-range boundaries that overlapped with standard Thiessen partitions of neighboring groups (Figures 2.2, 2.3, 2.4).

Space use and density.— Across all density conditions, home range and core area sizes ranged approximately 40-100 ha and 10-30 ha, respectively (Figures 2.5, 2.6). There was no significant site effect on home range or core area sizes (Home range model: F = 2.9, p = 0.09; Core area model: F = 2.5, p = 0.11; Table 2.2). Home ranges, but not core areas, were smaller during the second year of our study (Home range model: F = 3.3, p = 0.07; Core area model: F = 1.0, p = 0.31; Table 2.2). The interaction between density condition and season did not have a significant effect on home range or core area sizes (Home range model: F = 1.2, p = 0.31; Core area model: F = 1.1, p = 0.43), so we removed the interaction term to simplify model interpretation. Home range and core area sizes varied among density conditions (Home range model: F = 5.6, p = 0.004; Core area model: F = 3.5, p = 0.02) and seasons (Home range model: F = 10.2, p = <0.001; Core area model: F = 14.6, p = <0.001; Table 2.2). Average RCW home ranges and core areas were larger under low-density conditions than under medium and high-density conditions (Table 2.2; Figures 2.5, 2.6). Across home range and core area models, sizes were smallest during the breeding season, increased during the fledgling season, decreased during the post-fledgling season, and increased during the winter season (Figures 2.5, 2.6).

Foraging RCWs shared adjacent foraging habitat across all density conditions (Table 2.3, Figures 2.2, 2.3, 2.4). Spatial overlap between neighboring groups was greater on the Carolina Sandhills National Wildlife Refuge than Savannah River Site (Home range model: $F = 19.3$, $p = <0.001$; Core area model: $F = 29.5$, $p = <0.001$; Table 2.3). Across home range and core-use models, overlap estimates tended to be smallest during the breeding season, increased during the fledgling season, decreased slightly during the post-fledgling season, and increased during the winter season (Table 2.3, Figures 2.5, 2.6). The interaction between density condition and season had a significant effect on home range and core area overlap (Home range model: $F = 3.3$, $p = 0.004$; Core area model: $F = 3.2$, $p = 0.005$). Overlap of RCW home ranges during the winter season was lower for groups under low-density conditions than for groups under medium and high-density conditions (Table 2.3, Figures 2.5, 2.6). Overlap of RCW core areas during the post-fledgling season was lower under low and medium density conditions than under high-density conditions (Figure 2.6).

Space use and reproduction.—The interaction between density condition and home range size had a significant effect on clutch size (Home range model: $F = 3.6$, $p = 0.03$; Core-use model: $F = 1.02$, $p = 0.36$). Groups with larger home ranges under low-density conditions had smaller clutches than groups under medium and high-density conditions (Table 2.4, Figure 2.7). Additionally, the interaction between density condition and home range overlap had a significant effect on clutch size (Table 2.4). RCW clutch sizes increased with home range overlap under low-density conditions more so than clutch sizes of groups under medium and high-density conditions (Figure 2.7). We did not detect significant relationships between RCW group size and clutch size (Table 2.4).

Home range and core area sizes did not affect RCW nestling production or fledgling production (Tables 2.4, 2.5). Across all density conditions, nestling production decreased as home range overlap increased (Table 2.4, Figure 2.8). The interaction between home range overlap and neighboring group density condition had a significant effect on nestling production and fledgling production (Table 2.4). Fledgling production decreased with home range overlap under low and high-density conditions and increased slightly under medium density conditions (Table 2.4, Figure 2.8). Across all density conditions, larger groups had greater nestling and fledgling production (Table 2.4).

DISCUSSION

Our results show RCW home-ranges are distinct from defended territories, which have been conflated in previous RCW research; this is likely because most studies did not explicitly investigate frequencies of territorial behaviors or spatial overlap between neighboring groups, and thus were unable to distinguish defended territories from overlapping home ranges (Leonard et al. 2008, Anich et al. 2009, Cooper et al. 2014). That territorial interactions increased with density may even explain inconsistencies in the literature regarding relationships between RCW fitness and foraging habitat quality (Garabedian et al. 2014*b*). Territorial interactions can confound relationships between habitat quality and population density by influencing spacing patterns (Brown and Orians 1970), accessibility of limited resources including cavity trees and foraging habitat (Cox and McCormick 2016), and prospecting for potential dispersal destinations (Kesler and Walters 2012). With the rapid increase of many RCW populations over recent decades, concomitant increases in territorial interactions between neighboring groups could confound studies of resource selection used to develop standards of habitat quality (Walters 1991, James et al. 2001, Walters et al. 2002*b*, Macey et al. 2016), minimum area requirements to support viable RCW populations (Reed et al. 1988, Walters et al. 2002*a*, Zeigler and Walters 2014), and even retention of translocated RCWs in restored habitat (Cox and McCormick 2016).

Most inference on RCW home range dynamics and territoriality has been based on home range sizes without reference to variable use within home range boundaries. Despite use of kernel density methods to investigate RCW home ranges, the focus has been on size estimates and rarely has included internal structure or differential use within home range boundaries, which is a significant methodological limitation in studies of home range dynamics (Benhamou and Riotte-Lambert 2012). Minimum convex polygons fail to distinguish the internal structure of ranges, however, and as a consequence do not capture differential use needed to delineate territories within larger overlapping home ranges (Garrott and White 1990, Seaman and Powell 1996, Fieberg and Kochanny 2005, Schlicht et al. 2014). Moreover, cavity tree clusters were not consistently located at the center of RCW territories in our study, indicating future research should use caution if assuming cavity tree cluster represent the center of RCW territories (e.g., Cox and Engstrom 2001, Pasinelli and Walters 2002, Convery and Walters 2004, Schiegg et al. 2005, McKellar et al. 2014, 2015).

Critical habitat delineations made using Thiessen foraging partitions appear to reflect the competitive processes that form RCW territories, but not home ranges (Schlicht et al. 2014). Exclusive use of home ranges most often was reported in studies that assumed Thiessen partitions adequately represented RCW home range shapes and sizes (e.g., James et al. 1997, 2001, McKellar et al. 2014). High home range overlap indicated the absence of territoriality, but nearly exclusive core areas suggest RCW groups are reluctant to give up territorial boundaries that provide exclusive access to critical resources surrounding the cavity tree cluster (Nice 1941, Brown 1964, Husak 2000). This reluctance may be attributable to RCWs exhibiting partial territoriality to minimize costs of territorial defense, defending only core areas containing the cavity trees (DeLotelle and Epting 1988, Walters 1991). Defense of smaller intensively used habitat surrounding the cavity tree cluster suggests RCW populations likely are more tightly regulated by availability of cavity trees than availability of foraging habitat. Although mean home-range sizes decreased across density conditions in 2014, RCWs maintained stable core areas throughout the study, suggesting the importance of exclusive access to habitat in core areas is consistent over time because they contain the resource most limiting to RCW productivity.

The negative relationships between home range overlap and group fitness indicate RCWs can experience crowding effects that reduce fitness. Greater density of neighboring groups may reduce fitness (i.e., clutch size, nestling, and fledgling success) by increasing frequencies of territorial interactions, which likely limits the time allocated to rearing young. Other studies on Savannah River Site have reported similar relationships, where aggressive interactions between neighboring groups limited nestling provisioning (Johnston et al. 2004). Competition for food before and during egg laying can alter the amount of energy allocated to reproduction in many avian species (Lack 1966, Both 1998, 2000, Both et al. 2000, Brouwer et al. 2009). Female RCWs may be most affected prior to and during the breeding season when energy demands are greatest (Daan et al. 1988, Jackson and Parris 1995, Johnston et al. 2004). Yet, the relationships between overlap and fitness we observed differed from previous studies because we did not assume use was constant throughout home ranges

(Engstrom and Sanders 1997, Convery and Walters 2004). Engstrom and Sanders (1997) observed the greatest fledgling production observed for RCWs where home ranges overlapped up to 30%, and RCWs routinely foraged within home ranges and cavity tree clusters of neighboring groups. Visual inspection of our home ranges show a high degree of spatial overlap, supporting observations by Engstrom and Sanders (1997), but our results indicate differential use within overlapping areas is more important to fitness than total acreage of overlap.

Social interactions between neighboring RCW groups may provide short-term benefits that outweigh costs of competition with neighboring groups (Beletsky and Orians 1989). Positive relationships between clutch size and home range overlap under low-density conditions suggest an economical balance was achieved that allowed sample groups to monitor neighbors through vocalizations while remaining closer to the nest during the breeding season. With high quality foraging habitat, this type of balance could potentially be achieved under high density conditions even if RCWs intrude into cavity tree clusters or home ranges of neighboring groups (Engstrom and Sanders 1997). As a territorial resident species, repeated interactions between neighboring RCW groups may allow maintenance of shared territory borders while minimizing potential costly interactions (e.g., Ward and Schlossberg 2004). Obtaining information on neighboring groups could enhance fitness through greater vigilance in nest defense while minimizing antagonistic interactions with neighbors when energy demands and investment are very high (Wynne-Edwards 1962). Interaction behaviors by RCWs range from passive interactions with some vocalizations and no physical contact to aggressive physical altercations and vocalization (Ligon 1970). Passive interactions with some vocalization may allow neighboring groups to monitor shared borders while reserving aggressive physical altercations for the defense of core areas that contain cavity tree clusters. Other species use vocalizations as cues on the location of neighboring conspecifics and have been reported to dedicate more resources and time to reproduction as a result (Pasinelli and Walters 2002, Parejo et al. 2012, Farine et al. 2015, Expósito-Granados et al. 2016).

It is important to accurately describe patterns in space use near the periphery of home ranges for territorial resident species with complex social systems like the RCW, particularly in the context of space use that may be mediated by neighboring groups. Although we systematically followed foraging RCW groups throughout the year, some methodological aspects can be improved in future studies. Future research on RCW home-range behaviors should record locations at more frequent intervals (e.g., McKellar et al. 2015) or at each time a change in behavior is observed. For example, more frequent time intervals could be beneficial for studies of temporal interactions reliant on RCW group movement trajectories (e.g., Minta 1992, Benhamou and Riotte-Lambert 2012, Riotte-Lambert et al. 2015, Lambert et al. 2016). Recording RCW locations at each time behaviors change would be especially important to determine if crowding effects that RCW reduce fitness are driven by increased effort dedicated to territorial defense at the expense of provisioning nestlings. Temporal variation in RCW group movements would be particularly valuable in understanding how neighboring RCWs interact and partition space during the breeding season with respect to minimizing competitive interactions that can reduce nestling provisioning. Investigating simultaneous movements of neighboring RCWs could determine whether groups minimize competition by avoiding certain areas of overlapping home ranges when neighbors are present (e.g., Stamps 1991) or if neighboring groups forage in the same overlapping areas without overt aggression (Engstrom and Sanders 1997). As observations of intraspecific interactions can be difficult to collect, use of home-range overlap as a proxy for contact rates could be valuable for understanding the degree of territoriality in other resident birds as well (e.g., Millspaugh et al. 2004, Fieberg and Kochanny 2005, Robert et al. 2012, Cooper et al. 2014).

Relationships between conspecific density and home range dynamics are important components for development of effective conservation strategies for resident territorial birds like the RCW (Walters et al. 2002*a*, Schiegg et al. 2006, Aronsson et al. 2016). In the case of the RCW, home range overlap and territorial interactions that increase with conspecific density do not satisfy assumptions of Thiessen partitions to delineate RCW foraging habitat to individual groups. Based on our results, continued use of Thiessen foraging partitions will benefit RCW populations with comprehensive habitat protection, but managers should be aware that Thiessen partitions may overestimate the extent of defended territories and do not adequately account for increases in home range overlap with conspecific density that can reduce RCW group fitness.

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Table 2.1. Red-cockaded woodpecker home range behaviors observed for groups in low, medium, and high density conditions on the Savannah River Site (SRS) and Carolina Sandhills National Wildlife Refuge (CSNWR), South Carolina, between April 2013 and March 2015.

Site	Density	Year/Season	Relocation Summary[a]							Total
			Forage	Intra	Cavity	Inter	Rest	Incubation	Provision	
SRS North	Low	1/Breeding	2159	26	164	2	98	172	70	2691
		1/Fledgling	2015	45	53	0	37	0	26	2176
		1/Post-fledgling	2272	30	38	0	48	0	0	2388
		1/Winter	633	3	17	0	3	0	0	656
	Low	2/Breeding	1012	9	13	0	2	20	19	1075
		2/Fledgling	956	14	20	3	3	0	1	997
		2/Post-fledgling	960	5	16	1	12	0	0	994
		2/Winter	1074	13	8	1	13	0	0	1109
	Med	2/Breeding	1017	2	22	1	4	34	6	1086
		2/Fledgling	995	10	12	0	0	2	1	1020
		2/Post-fledgling	965	13	4	1	9	0	0	992
		2/Winter	980	16	12	0	12	0	0	1020
SRS South	Med	1/Breeding	2024	60	114	4	125	294	36	2657
		1/Fledgling	2017	53	127	0	46	0	2	2245
		1/Post-fledgling	2136	33	44	0	32	0	0	2245
		1/Winter	701	18	21	0	9	0	0	749

Table 2.1. Continued.

Site	Density	Year/Season	Relocation Summary[a]							Total
			Forage	Intra	Cavity	Inter	Rest	Incubation	Provision	
	High	2/Breeding	351	2	4	0	0	0	0	357
		2/Fledgling	980	18	29	0	1	0	1	1029
		2/Post-fledgling	986	25	12	0	9	0	0	1032
		2/Winter	1091	26	16	0	14	0	0	1147
CSNWR	High	1/Breeding	1177	53	75	8	111	68	105	1597
		1/Fledgling	1243	57	33	4	57	0	30	1424
		1/Post-fledgling	1354	20	25	2	43	0	0	1444
		1/Winter	905	17	7	0	16	0	0	945
	High	2/Breeding	1213	16	13	0	15	59	14	1330
		2/Fledgling	388	6	12	0	3	0	0	409
		2/Post-fledgling	819	8	3	0	13	0	0	844
		2/Winter	1129	50	10	1	31	0	0	1222
Total			33554	648	924	28	766	649	311	36880

[a] Forage = foraging; Intra = interactions with neighboring RCWs; Cavity = drilling resin wells, cavity maintenance, or breeding preparations; Inter = interspecific interactions; Rest = sedentary for >15 minutes; Incubation = incubation in cavity; Provision = feeding nestlings or fledglings.

Table 2.2. Mixed-effects analysis of variance comparing red-cockaded woodpecker home range and core area size estimates for groups in low, medium, and high density conditions on the Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina, between April 2013 and March 2015. The model intercepts represent the mean of home range and core area sizes for groups in high density conditions.

	Home range size		Core area size	
Parameter	β	95% CI	β	95% CI
(Intercept)	65.572 ***	52.14 – 79.00	13.523 ***	10.06 – 16.99
Year				
2014	-10.388 *	-20.31 – -0.46	-1.512	-4.10 – 1.07
Site				
Savannah River Site	-9.173	-25.41 – 7.07	-2.374	-6.60 – 1.85
Group size	5.301*	0.102 – 10.492	1.199	-0.164 – 2.563
Density				
Low	16.703 *	0.46 – 32.94	3.786 *	0.44 – 8.01
Medium	-3.425	-19.67 – 12.81	-0.606	-4.83 – 3.62
Season				
Fledgling	26.859 ***	14.658 – 39.061	8.672 ***	5.500 – 11.845
Post-fledgling	19.512 **	7.310 – 31.713	7.624 ***	4.452 – 10.797
Winter	35.663 ***	23.462 – 47.865	10.987 ***	7.814 – 14.159

* = $p < 0.05$ ** = $p < 0.01$ *** = $p < 0.001$

Table 2.3. Mixed-effects analysis of variance models comparing red-cockaded woodpecker home range and core area overlap estimates for groups in low, medium, and high density conditions on the Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina, between April 2013 and March 2015. The model intercepts represent the mean of home range and core area overlap for groups in high density conditions.

	Home range overlap		Core area overlap	
Parameter	*β*	95% CI	*β*	95% CI
(Intercept)	0.014 ***	0.008 – 0.019	0.000	-0.001 – 0.002
Year				
2014	-0.001	-0.003 – 0.002	0.001 **	0.000 – 0.002
Site				
Savannah River Site	-0.011 ***	-0.015 – -0.006	-0.003 ***	-0.005 – -0.002
Group size	<0.001	-0.002 – 0.002	<0.001	-0.001 – 0.001
Density				
Low	0.000	-0.008 – 0.009	0.003 *	0.001 – 0.005
Medium	0.000	-0.008 – 0.009	0.002 *	0.000 – 0.005
Season				
Fledgling	0.008 **	0.002 – 0.013	0.002 *	0.000 – 0.003
Post-fledgling	0.014 ***	0.008 – 0.019	0.006 ***	0.004 – 0.007
Winter	0.022 ***	0.016 – 0.027	0.002 **	0.001 – 0.004
Density : Season				
Low : Fledgling	0.001	-0.008 – 0.009	-0.001	-0.003 – 0.002
Medium : Fledgling	-0.001	-0.010 – 0.008	-0.001	-0.004 – 0.001
Low : Post-fledge	-0.007	-0.016 – 0.001	-0.005 ***	-0.007 – -0.003
Medium : Post-fledge	0.001	-0.008 – 0.009	-0.004 **	-0.007 – -0.002
Low : Winter	-0.017 ***	-0.026 – -0.009	-0.002	-0.005 – 0.000
Medium : Winter	-0.004	-0.013 – 0.004	-0.001	-0.004 – 0.001

* = $p < 0.05$ ** = $p < 0.01$ *** = $p < 0.001$

Table 2.4. Linear mixed-effects regression modeling variation in red-cockaded woodpecker 5-year mean fitness metrics (Clutch size, Nestling production, and Fledgling production) in response to group home range sizes, overlap, density condition, and group size for neighboring woodpecker groups on the Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina, between April 2013 and March 2015. The model intercepts represent the 5-year mean clutch size, nestling production, and fledgling production for groups in high density conditions.

	Clutch size		Nestling production		Fledgling production	
	β	SE	β	SE	β	SE
(Intercept)	2.87 ***	0.32	1.22 ***	0.33	0.74 *	0.30
Density						
Low	0.13	0.26	-0.92 ***	0.25	-0.66 **	0.21
Medium	-0.37	0.19	-0.51 **	0.19	-0.38 *	0.16
Size (ha)	0.02	0.14	0.07	0.14	0.03	0.12
Overlap	-0.19 *	0.09	-0.37 ***	0.09	-0.34 ***	0.08
Group size	0.20	0.11	0.42 ***	0.11	0.43 ***	0.10
Density : Size						
Low : Size	-0.37 *	0.18	0.09	0.18	0.18	0.16
Medium : Size	0.17	0.20	0.14	0.20	0.12	0.17
Density : Overlap						
Low : Overlap	0.74 *	0.31	0.16	0.31	0.15	0.27
Medium : Overlap	-0.34	0.25	0.19	0.25	0.41	0.21

* = $p < 0.05$ ** = $p < 0.01$ *** = $p < 0.001$

Table 2.5. Linear mixed-effects regression modeling variation in red-cockaded woodpecker fitness metrics (Clutch size, Nestling production, and Fledgling production) in response to group core area sizes, overlap, density condition, and group size for neighboring woodpecker groups on the Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina, between April 2013 and March 2015. The model intercepts represent the 5-year mean clutch size, nestling production, and fledgling production for groups in high density conditions.

	Clutch size		Nestling production		Fledgling production	
	β	SE	*β*	SE	*β*	SE
(Intercept)	2.70 ***	0.38	1.14 **	0.38	0.73 *	0.34
Density						
Low	-0.20	0.18	-0.65 ***	0.18	-0.39 *	0.16
Medium	-0.18	0.18	-0.34	0.19	-0.27	0.16
Size (ha)	-0.21	0.19	0.00	0.19	-0.09	0.17
Overlap	-0.07	0.08	-0.11	0.08	-0.07	0.07
Group size	0.24	0.13	0.38 **	0.13	0.38 **	0.12
Density : Size						
Low : Size	0.05	0.21	0.20	0.21	0.29	0.18
Medium : Size	0.29	0.23	0.09	0.23	0.22	0.21

* = $p < 0.05$ ** = $p < 0.01$ *** = $p < 0.001$

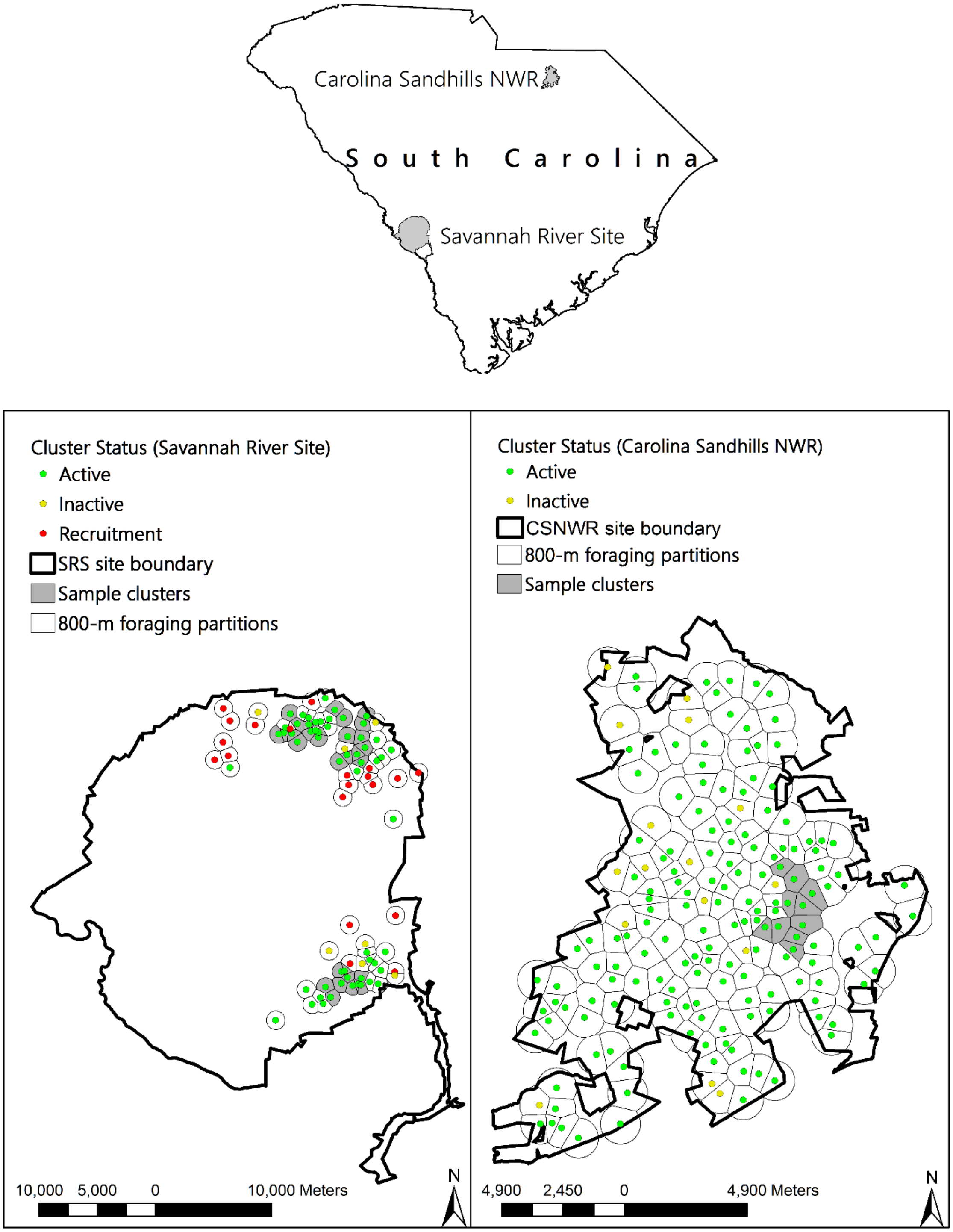

Figure 2.1. The spatial distribution and status of red-cockaded woodpecker cavity tree clusters on Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina, USA, in 2013.

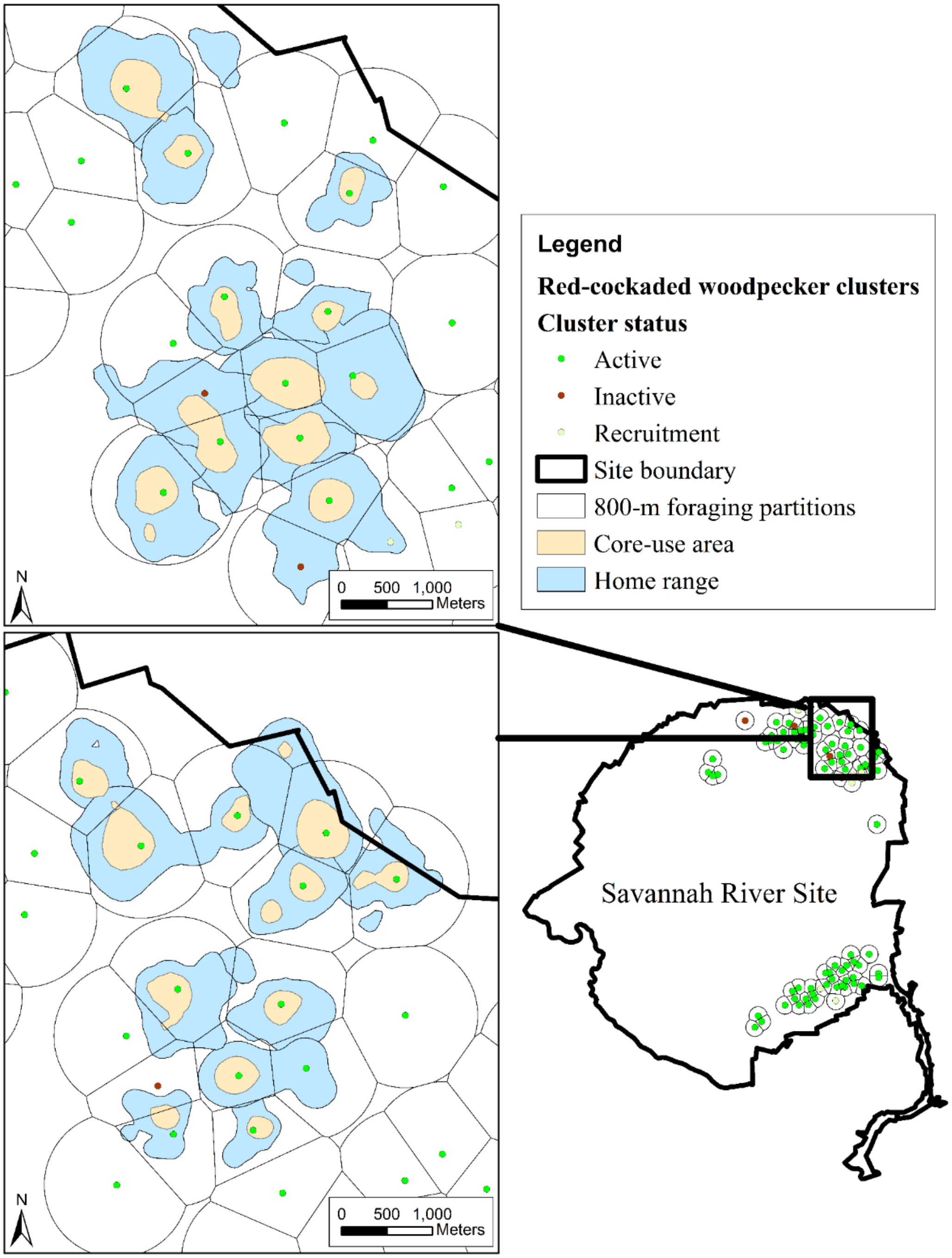

Figure 2.2. Annual core-area and home-range boundaries for red-cockaded woodpecker groups under low density conditions on the Savannah River Site, South Carolina. Top and bottom map panels represent space-use estimates from years 2013 and 2014 of the study, respectively.

Figure 2.3. Annual core-use and home-range boundaries for red-cockaded woodpecker groups under medium density conditions on the Savannah River Site, South Carolina. Top and bottom map panels represent space-use estimates from 2014 and 2013, respectively.

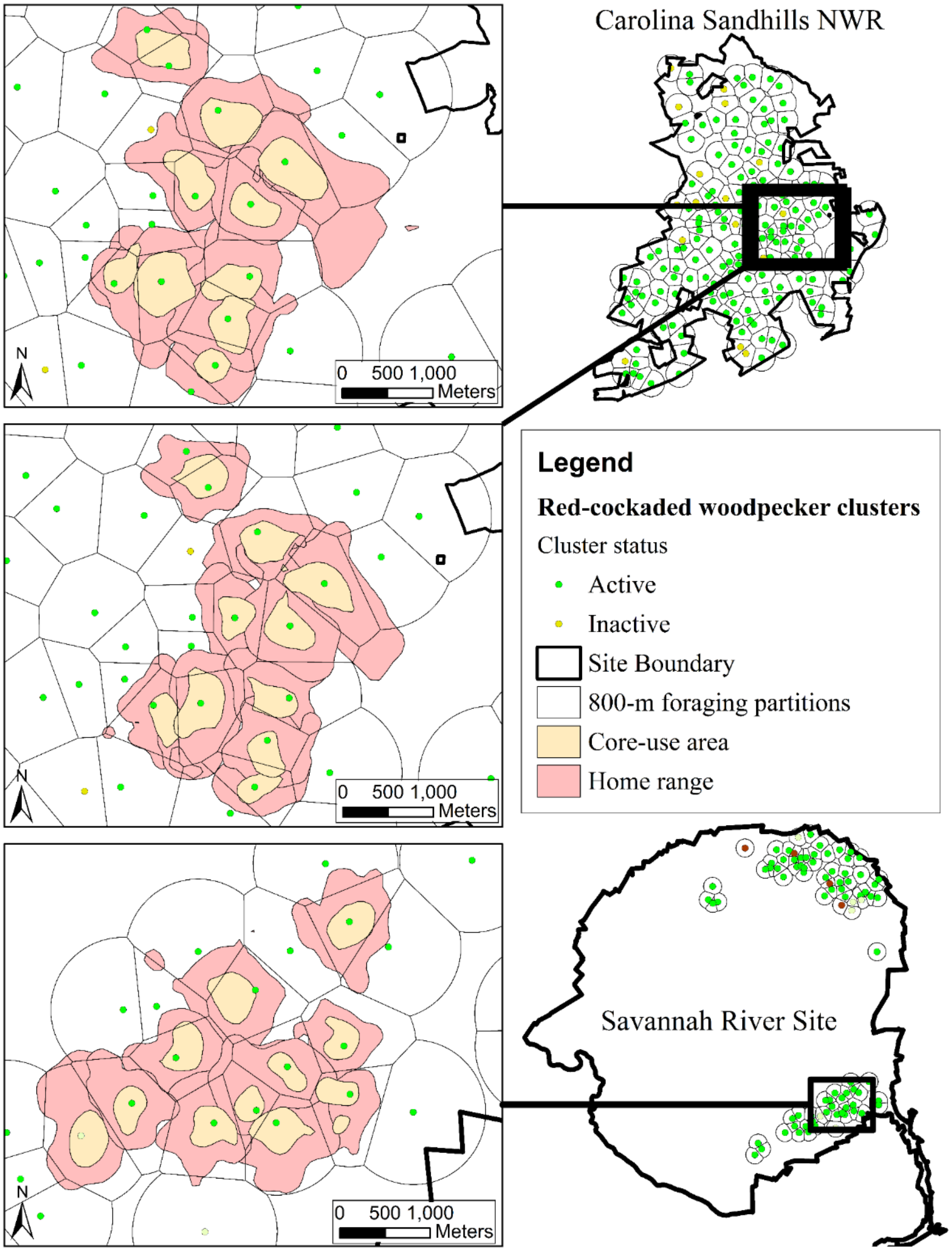

Figure 2.4. Annual core-use and home-range boundaries for red-cockaded woodpecker groups under high density conditions population on the Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina. Top and middle map panels represent boundaries during 2013 and 2014, respectively, on the Carolina Sandhills National Wildlife Refuge. The bottom map panel represents boundaries during 2014 on the Savannah River Site.

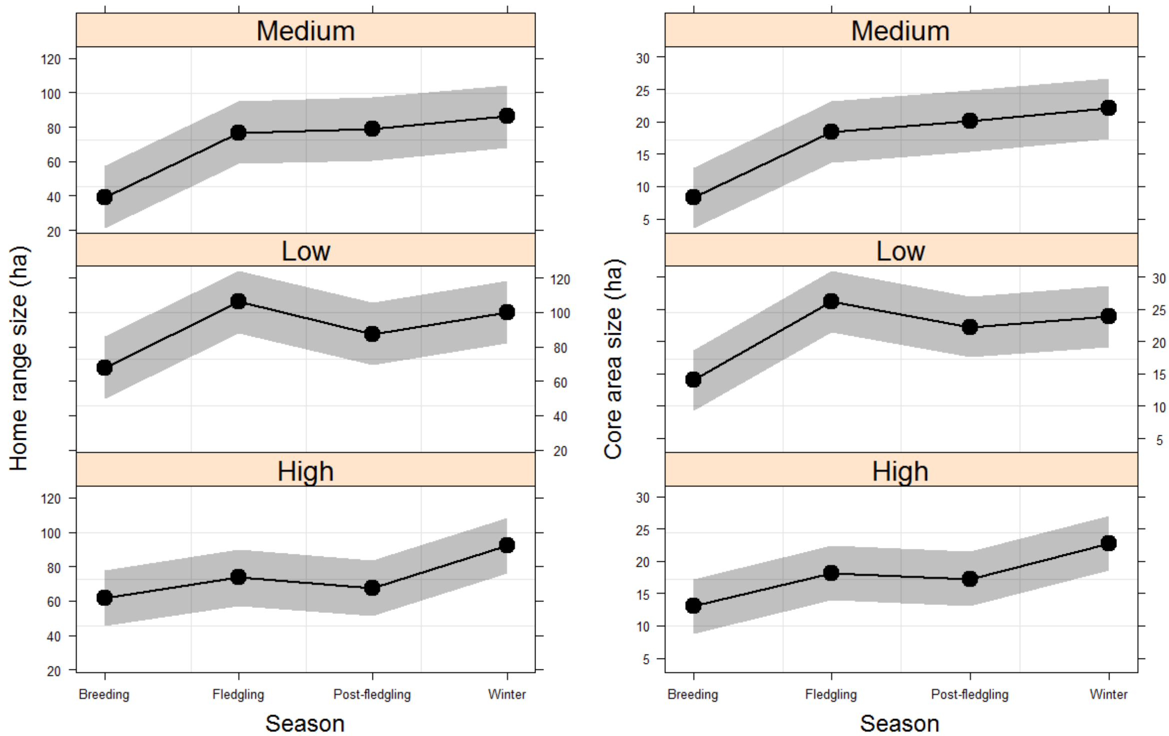

Figure 2.5. Plot illustrating the relationship between red-cockaded woodpecker home range and core area sizes and season across low, medium, and high group density conditions. Black circles connected by trend lines represent mean size estimates and gray bands represent 95% confidence intervals.

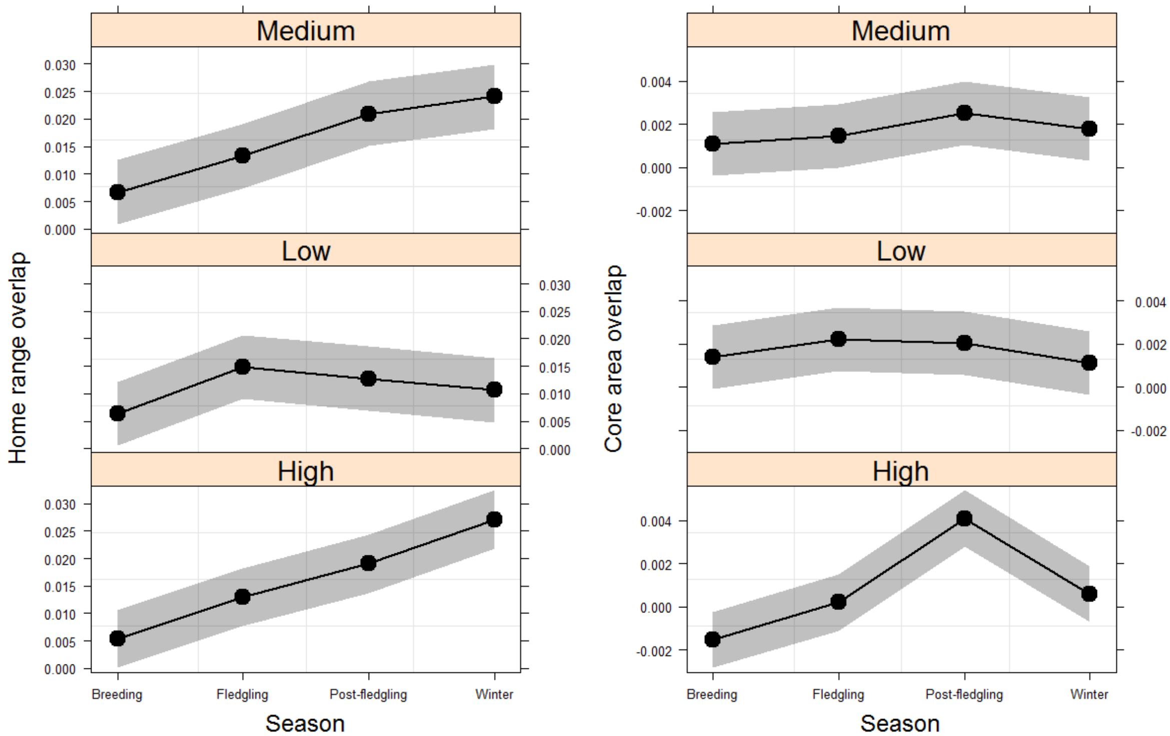

Figure 2.6. Plot illustrating the relationship between red-cockaded woodpecker home range and core area overlap and season across low, medium, and high group density conditions. Black circles connected by trend lines represent mean size estimates and gray bands represent 95% confidence intervals.

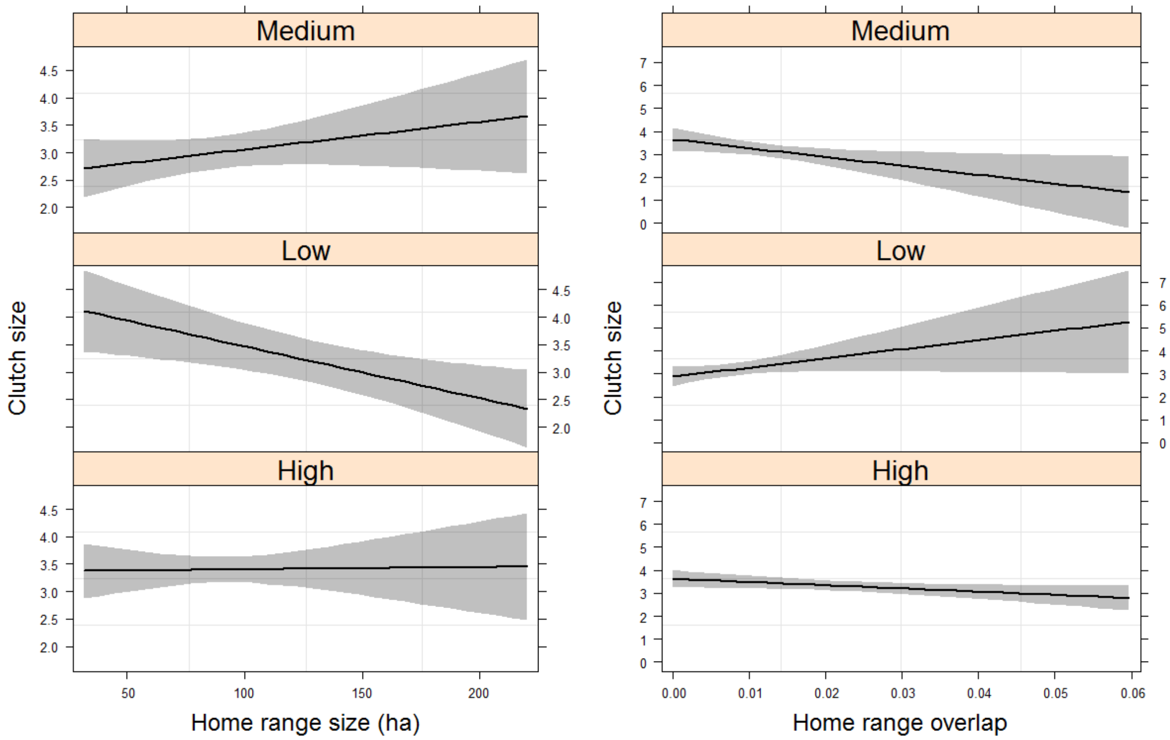

Figure 2.7. Plot illustrating the interaction between home range area and overlap on 5-year mean clutch size of red-cockaded woodpecker groups under low, medium, and high neighboring group density conditions on the Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina between 2013 and 2014. Black lines represent fitted interaction effects and gray bands represent 95% confidence intervals.

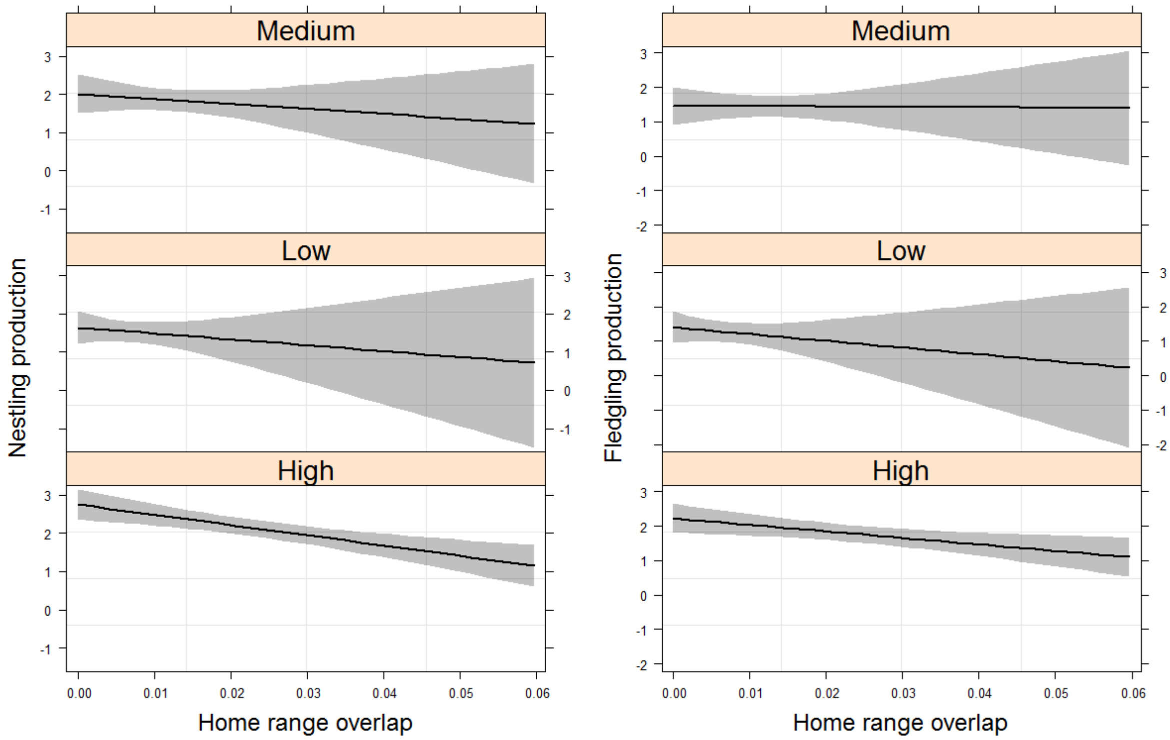

Figure 2.8. Plot illustrating the relationship between 5-year mean nestling and fledgling production and home range overlap of red-cockaded woodpecker groups under low, medium, and high group density conditions on the Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina between 2013 and 2014. Black lines represent fitted lines and gray bands represent 95% confidence intervals.

CHAPTER 3: Modeling Fine-grained Resource Use to Inform Strategic Management of an Endangered Woodpecker

ABSTRACT

Advances in LiDAR remote sensing technology offer new opportunities to validate and refine habitat models to guide woodland bird conservation, particularly when integrated with population level data such as population density and social behaviors. We integrated fine-grained LiDAR-derived habitat data, the spatial distribution of cavity trees, and spatially-explicit behavioral observations in a multiscale habitat model to determine the relative importance of conspecific density, intraspecific interactions, and the distribution of nest sites on habitat use by red-cockaded woodpeckers (*Leuconotopicus borealis*; RCW) on two sites in South Carolina, USA. We evaluated candidate models using information theoretic methods and applied the top model to project habitat use with temporally independent RCW home range data. Top multiscale models included effects of neighboring group density, distance to group's cavity tree cluster, and number of cavity tree starts within 200-m of RCW foraging utilization distributions (UDs) and effects of average annual frequency of intraspecific interactions within 400-m of RCW foraging UDs. The most parsimonious scale-specific model for 15 of 20 RCW sample groups included covariates for the number of neighboring groups within 200 m and LiDAR-derived habitat with $\geq$22 cm dbh/ha pines $\geq$35.6 cm dbh/ha, $\geq$2.3 m^2/ha basal area (BA) of pines $\geq$25.4 cm dbh, <0.4 m^2/ha basal area of hardwoods <22.9 cm dbh/ha, and <10% hardwood canopy cover. These results suggest neighboring group location was the most important variable predicting habitat use once a minimal set of structural habitat thresholds were reached, and that placing recruitment cavity trees as little as 200 m to 400 m from foraging partitions of neighboring clusters may be key to successful reintroduction efforts. The presence of neighboring groups likely provides cues

to foraging RCWs that facilitate prospecting prior to juvenile dispersal and, to a lesser extent, high quality forage resources. Careful consideration of fine-grained spatial distribution of neighboring groups in potential foraging habitat may improve managers' ability to mitigate isolation of RCW groups that negatively affects fitness across the species' range, and potentially increase overall RCW density on management areas.

INTRODUCTION

Effective wildlife conservation requires knowledge of factors determining the distribution of animals across space and time (Aarts et al. 2013). Increasing pressures on wildlife populations from habitat loss and degradation have made spatially explicit representations of habitat relationships a critical conservation tool, especially for recovery of endangered species (Rotenberry et al. 2006). More specifically, spatially explicit maps of wildlife habitat relationships have proven to be valuable tools for conservation and management applications, including delineation and prioritization of species' critical habitat and reserve selection (Graf et al. 2005, 2009, Guisan et al. 2013, Ackers et al. 2015, Denoël and Ficetola 2015).

Advances in remote sensing technology offer new opportunities to validate and refine species-habitat models, particularly for specialist species that respond to fine-grained variation in forest structure (Graf et al. 2009, Ficetola et al. 2014, He et al. 2015, Froidevaux et al. 2016, Sesnie et al. 2016). Light distance and ranging (LiDAR) technology has become an invaluable tool for modeling and mapping habitat structure across broad extents while retaining fine-grained three-dimensional detail (Vierling et al. 2008, Hudak et al. 2009, Dassot et al. 2011, Hansen et al. 2014, Vogeler and Cohen 2016). High-resolution LiDAR-based habitat models have improved the ability to produce habitat maps at spatial scales relevant to species' recovery and management programs (Garabedian et al. 2014*a*). These high-resolution habitat maps allow greater spatial precision in prioritizing local areas for conservation of species with narrow niches and limited habitat (Graf et al. 2009, García-Feced et al. 2011, Smart et al. 2012, Farrell et al. 2013, Ackers et al. 2015). Further, LiDAR has contributed to a greater understanding of scale-dependencies in species' habitat use because it permits derivation of novel habitat covariates that can be summarized across a continuum of spatial grains and extents (Seavy et al. 2009, Weisberg et al. 2014, Hill and Hinsley 2015, Barnes et al. 2016, Huber et al. 2016).

High-resolution animal location data, as from global positioning system (GPS) technology, have fostered new opportunities to link woodland bird space use to spatially-explicit resources using animal utilization distributions (UD; Worton 1989, Marvin et al. 2016). A main advantage of UDs is the ability to explore species-habitat relationships as continuous processes, offering new opportunities to contrast relative importance of specific resources at multiple spatial extents (Millspaugh et al. 2006, Masse et al. 2014, Denoël and Ficetola 2015, McGarigal et al. 2016). For example, modeling species' distributions has been used to inform endangered species management by identifying the extent at which species' response to a specific feature is strongest (Campioni et al. 2013, Marvin et al. 2016, Murgatroyd et al. 2016). Additionally, identifying the most intensively used areas within utilization distributions may also elucidate features most limiting to species that maintain all-purpose home-ranges throughout the year (Ford 1983, Samuel et al. 1985, Stanton et al. 2014).

Social behaviors (e.g., territoriality) must be considered alongside fine-grained vegetation metrics for many species, particularly those with narrow niches and complex reproductive strategies (Guisan et al. 2013). Habitat variables alone may not provide adequate information for reserve design for populations of resident cavity nesting birds because they may not account for how the location of nest sites influences habitat use (Newton 1991, 1994, 1998, Both and Visser 2003, Denoël and Ficetola 2015). This is especially true when habitat quality is also determined by the local distribution of conspecifics and features, such as cavity trees, critical to individual reproduction and survival

(Pulliam et al. 1992, Denoël and Ficetola 2015). For resident woodland birds like the cooperatively breeding brown-headed nuthatch (*Sitta pusilla*), the density and distribution of conspecifics and snags could be key to understanding why the species selects patches of atypical habitat in restored areas, in turn influencing the extent of potential habitat (Stanton et al. 2015).

Conservation of the federally endangered red-cockaded woodpecker (*Leuconotopicus borealis*; RCW) would benefit from standards of habitat quality that integrate traditional fine-grained habitat metrics (e.g., foraging habitat thresholds), the spatial distribution of cavity trees, and social behaviors (e.g., territoriality). Because foraging RCWs may avoid or be excluded from foraging habitat within the vicinity of neighboring group cavity tree clusters, understanding the scale-dependent effects of local neighboring group density, territorial interactions, and distance to cavity tree clusters could aid managers in identifying the most appropriate spatial scale for RCW management. The role of neighboring group density in RCW habitat use might be more important than previously recognized, especially for RCW occupying artificial cavities in restored or intensively managed foraging habitat, as reported in other studies of other territorial resident woodland birds (e.g., Stanton et al. 2015). For example, if foraging RCWs respond positively to the distribution and density of neighboring groups, strategic installation of recruitment clusters within a minimum distance of occupied cavity tree clusters could mitigate effects of isolation that can limit RCW reproductive success or dispersal (Cox and Engstrom 2001, Pasinelli et al. 2004, Cox and McCormick 2016).

Our objective was to integrate high-resolution LiDAR-derived habitat data, the distribution of cavity trees and cavity tree starts, home-range behaviors (e.g., foraging, intraspecific interactions), and population density in a spatially-explicit model of space use and assess the relative importance of key habitat requirements (e.g., structural thresholds for pines $\geq$35.6 cm dbh, pines $\geq$25.4 cm dbh, hardwoods <22.9 cm dbh, and hardwood canopy cover), social interactions (e.g., frequency of intraspecific interactions), and population density (e.g., distribution of active RCW cavity tree clusters) to foraging RCWs. Specifically, we: 1) ranked multi-scale effects of social interactions, key discrete resources, and population density on fine-grained space use by foraging RCWs; 2) evaluated support among multiple spatially-explicit candidate models describing variation in RCW utilization distributions as a function of LiDAR-derived foraging habitat thresholds, neighboring group density, and home range behaviors; and 3) validated the top candidate model using temporally independent data collected on Savannah River Site and generated maps of potential RCW habitat with associated error estimates.

STUDY SITE

The Savannah River Site, an 80,267-ha National Environmental Research Park owned and operated by the U.S. Department of Energy, is located on the Upper Coastal Plain and Sandhills physiographic provinces in South Carolina, USA. The Savannah River Site is characterized by sandy soils and gently sloping hills dominated by pines (*Pinus* spp.) with scattered hardwoods (Kilgo and Blake 2005). Prior to acquisition by the U.S. Department of Energy in 1951, the majority of the Savannah River Site was maintained in agricultural fields or recently had been harvested for timber (White 2005). The U.S. Department of Agriculture Forest Service has managed the natural resources of the Savannah River Site since 1952 and reforested the majority of the site (Imm and McLeod 2005). Approximately 53,014 ha of the Savannah River Site is now re-forested with artificially regenerated stands of loblolly (*P.*

taeda), longleaf (*P. palustris*), and slash (*P. elliottii*) pines with an additional 2,832 ha with pine-hardwood mixtures (Imm and McLeod 2005). The remaining 27,000 ha of forested area on the Savannah River Site includes bottomland hardwoods, forested wetlands/riparian areas, and mixed-hardwood stands (Imm and McLeod 2005). Mixed pine-hardwood stands on Savannah River Site typically include a mixture of longleaf pine, loblolly pine, and *Quercus* spp. Midstory trees that reach the subcanopy typically are small *Quercus* spp., but there are mixtures of midstory hardwoods that also include sand hickory (*Carya pallida*), sweetgum (*Liquidambar styraciflua*), and sassafras (*Sassafras albidum*).

In conjunction with the Department of Energy, the U.S. Department of Agriculture Southern Research Station began management and research on the RCW in 1984 with the objective to restore a viable population on the Savannah River Site. Under intensive management since 1985, the RCW population has grown from three groups of four birds (Johnston 2005) to 91 groups of over 250 birds (T. Mims, *pers. comm.*). Management of RCW foraging habitat on Savannah River Site has included prescribed fire and other methods to control hardwood midstory, construction of recruitment clusters, and aggressively protecting existing cavity trees (Allen et al. 1993, Haig et al. 1993, Franzreb 1997, Edwards and Costa 2004). The Savannah River Site RCW population is designated as a secondary core population in the South Atlantic Coastal Plain recovery unit (U.S. Fish and Wildlife Service 2003). All RCWs at the Savannah River Site are uniquely color-banded by U.S. Forest Service personnel as part of ongoing monitoring. Additionally, RCW group observations and nest checks were conducted during each nesting season since 1985 to determine clutch size, nestling production, fledgling production, and group size for each cluster.

The Carolina Sandhills National Wildlife Refuge, one of 14 Land Management and Research Demonstration areas managed by the U.S. Fish and Wildlife Service, is located on the Atlantic Coastal Plain and Piedmont Plateau physiographic provinces, South Carolina, USA. The Carolina Sandhills National Wildlife Refuge is characterized by sandy soils dominated by upland, xeric pine woodlands. The refuge is approximately 19,364 ha, including 14,164 ha of predominantly longleaf pine-turkey oak (*P. palustris-Quercus cerris*) cover (U.S. Fish and Wildlife Service 2010). The refuge harbors 150 active RCW clusters, representing the largest RCW population on U.S. Fish and Wildlife Service lands. As part of ongoing monitoring efforts, Carolina Sandhills National Wildlife Refuge personnel monitor nests and band nestlings with aluminum bands and unique combinations of color bands.

METHODS

Our approach involved a series of sequential steps. First, we visually tracked individual RCW groups and recorded foraging locations (home-range follows) to estimate annual UDs for each RCW group. Next, we conducted a multiscale analysis to identify the spatial scale(s) at which intraspecific interactions, distance to cavity tree clusters, the number of cavity tree starts (i.e., cavities being excavated by RCWs but that have not been completed), and density of neighboring groups were most influential on RCW space use. We then fit resource utilization functions (RUFs; Hepinstall et al. 2003, Marzluff et al. 2004, Millspaugh et al. 2006, Kertson et al. 2011) to model RCW space use as a function of LiDAR-derived habitat data and scale-specific covariates for intraspecific interactions, distance to cavity tree clusters, and the number of cavity tree starts identified most important in multiscale models. After comparison of candidate RUF models using information theoretic methods, we used the top model to project habitat use with independent home range data for RCW groups collected on Savannah River Site in 2014. Finally, we validated the top RUF model by comparing predicted and observed habitat use and an assessment of prediction error.

Home-range data.— We collected home-range data for a sample of 44 foraging RCW groups on the Savannah River Site (n = 34) and Carolina Sandhills NWR (n = 10; Figure 3.1). We tracked individual RCW groups minimally over a 4-hour period, recording location fixes at 15-min intervals (Franzreb 2006), twice a month between March 2013 and April 2015. We recorded at least 15 location fixes throughout the day during each follow, thus providing >30 relocations per month. We considered follows incomplete if we recorded <15 location fixes during a single day; we repeated incomplete follows at a later date of the same month. Home-range follows consisted of sustained visual contact with individuals of the sample group beginning when they left their roosts in the morning and continuing until contact with the birds was lost, or until terminated due to inclement weather or management activities that precluded site access (e.g., prescribed burning). In addition to location fixes, we recorded basic behavior (foraging, resting, cavity work, feeding nestlings, or interspecific interactions) at each 15-min interval. RCW group members tend to forage in close proximity to one another, even concurrently in the same tree (Franzreb 2006), so we used location fixes for the breeding male of each sample group to represent movement of the entire group.

Utilization distributions.— We used fixed-kernel density methods and the reference bandwidth to estimate annual UDs for each of the 44 RCW sample groups. Following Garabedian et al. (2014*a*), we estimated UDs for individual RCW groups on 80- x 80-m resolution grids that matched the spatial resolution of LiDAR-derived habitat data used in previous RCW habitat research on the Savannah River Site. We superimposed 99% UD-volume contours on the 80- x 80-m grid to delineate foraging habitat available to individual

RCW groups, which also ensured the spatial grids on which RCW UDs were estimated remained consistent across individual groups. Additionally, we superimposed 99% UD-volume contours on 800-m Thiessen foraging partitions recommended by the USFWS for allocating foraging habitat to individual RCW groups. Using this method, we created 800-m radii circular foraging partitions centered on a groups' cavity tree cluster to delineate habitat available to individual groups. In situations where circular partitions would overlap (i.e., cavity tree clusters are < 800 m apart), we used Thiessen polygons to create mutually exclusive partitions that delineate an area around each cavity tree cluster such that the boundaries equally divide space between all neighboring RCW groups (hereafter, Thiessen partitions; Lipscomb and Williams 1996).

Spatially-explicit covariates.— We used the Spatial Analyst Extraction tool to create the spatially-explicit dataset required to fit RUFs (ESRI 2014). We output all spatial covariates onto an 80- x 80-m resolution grid to match the grids on which we estimated RCW UDs. Following Garabedian et al. (2014*a*), we used high-resolution LiDAR-derived estimates of forest structure to quantify the amount and condition of foraging habitat available to individual RCW groups within 99% UD-volume contours. We used 4 site-specific structural habitat thresholds (Chapter 1) to define the suite of LiDAR-derived habitat covariates fit in subsequent models (Table 3.1).

We summarized the average annual frequency of intraspecific interactions, distance to groups' respective cavity tree cluster, and the number of neighboring groups across multiple spatial extents for use in multiscale analyses. We compiled multiscale data by averaging covariate values in a moving window analysis and assigned scale-specific averages to individual 80- x 80-m grid cells within 99% UD contours. We created spatial data layers for: 1) the number of neighboring RCW groups within 200, 400, 800, 1600, and 2000-m circular windows centered on each grid cell within 99% UD contours; 2) the average annual frequency of interactions between neighboring RCW groups within 100-, 200-, 300-, and 400-m circular windows centered on each grid cell within 99% UD contours; 3) the number of cavity tree starts within 200-, 400-, 600-, and 800-m circular windows centered on each grid cell within 99% UD contours; and 4) Euclidean distance to a group's cavity tree cluster from individual grid cells within the group's UD binned at 200-m intervals within 99% UD contours (Table 3.1).

Univariate resource utilization functions.— We fit univariate RUFs for each RCW group to rank effects for the number of neighboring RCW groups, number of cavity tree starts, distance to group cavity tree clusters, and average annual frequency of intraspecific interactions summarized across multiple spatial extents at the 80- x 80-m resolution (Table 3.1). We used Akaike's Information Criteria (AIC) and ΔAIC values to rank support for univariate RUF candidate models (Akaike 1974, Burnham and Anderson 2004). We first ranked AIC values for each candidate model fit for individual RCW groups to rank models at the individual-group level. We then summed the frequency of top models at the individual-group level to identify the most parsimonious scale-specific responses to the number of neighboring RCW groups, number of cavity tree starts, distance to group cavity tree clusters, and average annual frequency of intraspecific interactions. We retained covariates summarized at the most parsimonious spatial extent for use in subsequent scale-specific multivariate RUFs.

Multivariate resource utilization functions.—We fit scale-specific multivariate RUFs that included measurements of nearest neighboring groups, cavity tree starts, Euclidian distance to groups' respective cavity tree cluster, and LiDAR-derived structural habitat thresholds as independent variables. Because we did not have LiDAR-derived habitat data for the Carolina Sandhills NWR, we only fit multivariate RUFs for the groups followed on the Savannah River Site in 2013 (n = 20) and 2014 (n = 34). We used the same approach for model selection as described for univariate RUFs. We used population averages of unstandardized beta coefficients from the top candidate RUF to predict habitat use and to map potential RCW habitat based on independent home range data collected for RCW groups on the Savannah River Site in 2014 (n = 34). We fit RUFs using the R statistical environment (R Development Core Team 2015) and the contributed package "ruf" (Handcock 2015). We mapped predicted habitat use and associated prediction error on an 80- x 80-m grid using the Raster Calculator in ArcGIS (ESRI 2014).

RESULTS

Utilization distributions.—On average, we used 696 foraging relocations (SE: ±57 relocations) to estimate RCW foraging UDs. Total area of foraging habitat available to RCWs within boundaries of 99% UD volume contours averaged 135 ha and ranged from 48-304 ha. The reference bandwidths estimated for individual RCW group foraging UDs averaged 83 m (median: 80 m; range: 41.5, 151.5 m).

Spatially-explicit covariates.— We documented 99 cavity tree starts between 2013 and 2014 during home-range follows; average number of cavity tree starts per 80- x 80-m UD grid cell was highest and lowest at 800-m and 200-m spatial extents, respectively (Table 3.2). We observed 648 intraspecific interactions between 2013 and 2014; average frequency of intraspecific interactions per grid cell was highest at 400-m and lowest at 200-m (Table 3.2). The number of nearest neighboring groups per UD grid cell was highest at 2000-m and lowest at 200-m on the Carolina Sandhills NWR and on the Savannah River Site, respectively (Table 3.2). RCW groups foraged between 48 m and 250 m away from their cavity tree clusters on both sites (Table 3.2).

Univariate resource utilization functions.— Multiscale models indicated that fine-grained factors at 200-m and 400-m extents were the most important scales for predicting RCW habitat use. Number of neighboring groups was most parsimonious at the 200-m spatial extent and had positive effects ($\beta = 36.451$; SE = 1.596) on RCW space use (Table 3.3). Average annual frequency of intraspecific interactions was most parsimonious at the 400-m extent and did not affect ($\beta = 2.032$; SE = 2.079) RCW space use (Table 3.3). Euclidian distance to a group's cavity tree cluster was most parsimonious at the 200-m extent and had positive effects ($\beta = 0.181$; SE = 0.001) on RCW space use (Table 3.3). Cavity tree starts was most parsimonious at the 200-m extent and had positive effects ($\beta = 0.075$; SE = 0.001) on RCW space use (Table 3.3). We retained the covariates representing the number of neighboring groups within 200-m of UD grid cells, number of cavity tree starts within 200-m of UD grid cells, the average annual frequency of intraspecific interactions within 400-m of UD grid cells, and Euclidian distance to group's cavity tree cluster within 200-m of UD grid cells for use in subsequent multivariate RUFs that included additive effects of LiDAR-derived habitat thresholds (Table 3.4, Figures 3.2, 3.3, 3.5).

Multivariate resource utilization functions.— The model selection clearly indicated that almost immediate adjacency to extant cavity trees was the most important predictor of RCW habitat use once baseline vegetation attributes existed in an area (Table 3.5). The most parsimonious scale-specific RUF for 15 of 20 RCW sample groups included covariates for the number of neighboring groups within 200-m of UD grid cells and LiDAR-derived habitat thresholds (Table 3.5). We detected positive effects of *k* nearest neighboring groups (β = 30.87; 95% CI = 14.15 – 47.58) and LiDAR-derived habitat with $\geq$22 pines $\geq$35.6 cm dbh/ha (β = 5.98; 95% CI = 1.41 – 5.98), $\geq$2.3 m^2/ha basal area (BA) of pines $\geq$25.4 cm dbh (β = 4.84; 95% CI = 3.98 – 5.70), <0.4 m^2/ha BA of hardwoods <22.9 cm dbh (β = 5.96; 95% CI = 2.02 – 9.90), and <10% hardwood canopy cover (β = 11.59; 95% CI = 6.85 – 16.33; Table 3.5). The most parsimonious scale-specific RUF for 3 of 30 RCW sample groups included Euclidian distance to a group's cavity tree cluster within 200-m of a UD grid cell and LiDAR-derived habitat thresholds (Table 3.5). We detected negative effects of distance to group's cavity tree cluster (β = -0.123; 95% CI = -0.138 – -0.107) and positive effects LiDAR-derived habitat $\geq$2.3 m^2/ha BA of pines $\geq$25.4 cm dbh (β = 2.52; 95% CI = 0.03 – 5.01), <0.4 m^2/ha BA of hardwoods <22.9 cm dbh (β = 6.17; 95% CI = 3.10 – 9.22), and <10% hardwood canopy cover (β = 8.56; 95% CI = 5.96 – 11.16) (Table 3.5). Scale-specific RUFs fit with LiDAR-derived habitat thresholds, and covariates for intraspecific interactions within 400-m of UD grid cells or cavity tree starts within 200-m of UD grid cells were each the most parsimonious model for 1 of 20 RCW sample groups (Table 3.5).

We used averaged unstandardized coefficients from RUF models with the number of neighboring groups within 200-m of UD grid cells and LiDAR-derived habitat thresholds to predict habitat use for 34 foraging RCWs followed in 2014. The distribution of potential RCW habitat predicted using independent RCW data was largely protected by 800-m Thiessen foraging partitions. Some areas beyond the boundaries of RCW foraging partitions had relatively high predicted use by foraging RCWs (Figures 3.6, 3.7).

DISCUSSION

Once baseline vegetation thresholds were satisfied the distribution of neighboring groups within 200 and 400 meters of RCW home ranges was the predominant variable predicting habitat use by foraging RCWs. Our results suggest fine-grained habitat use by foraging RCWs may be mediated by local population density such that RCWs may use the presence of neighboring groups as a proximate indicator of habitat quality. Foraging RCWs may use the presence of neighbors as a cue for high-quality foraging habitat and food resources that may improve fitness (Jordan 2002). However, arthropod prey availability may not be the mechanism driving aggregations of neighboring RCWs in high-quality foraging habitat detected in our study. Prolonged episodes of arthropod exhaustion on pines selected by foraging RCWs are likely rare due to movement of arthropods up the pine bole from the understory (Hanula and Franzreb 1998), so it is unlikely RCWs would use neighboring groups as a cue for abundant arthropod prey items. Previous research demonstrates RCWs forage on a variety of arthropods, but select similar arthropod prey to provision nestlings on sites representing high and low-quality habitat (Hanula and Franzreb 1998, Hanula and Engstrom 2000, Hanula et al. 2000, Horn and Hanula 2008). Because arthropod prey available to foraging RCWs does not appear to fluctuate extensively over space or time, the presence of neighboring groups may only have marginal value as cues on the location of rich arthropod prey resources or high-quality foraging habitat.

Alternatively, foraging RCWs may aggregate in areas with more neighboring groups to gain cues on neighbors that facilitate prospecting behaviors prior to juvenile dispersal (Kesler et al. 2010, Cox and Kesler 2012*a*, *b*, Kesler and Walters 2012). Natal dispersal decisions are contingent on social and environmental conditions on and around the natal territory (Pasinelli and Walters 2002), which could be why we detected strong positive responses to neighboring groups and foraging habitat structure by foraging RCWs. Given dispersing RCWs typically remain within 4 neighboring groups of their natal territory (Daniels and Walters 2000), it is likely dense aggregations of neighboring groups are advantageous for dispersing RCWs by increasing the likelihood of finding a suitable destination group (Pasinelli et al. 2004). Daniels (1997) reported dispersal distances tend to be larger under low population densities, which suggests the distribution and density of neighboring RCW groups has a greater impact on habitat use and movements by RCWs than foraging habitat structure. Because larger RCW groups have consistently been correlated with increased reproductive success (Khan and Walters 2002), and approximately 50% of male fledglings and nearly all female fledglings disperse or die (Walters et al. 1988), isolation from neighboring groups could indirectly limit RCW group size and consequently reduce group reproductive success. If dispersing RCWs are unable to find suitable destination groups, which often occurs in isolated groups (U.S. Fish and Wildlife Service 2003), the benefits helper individuals confer on population persistence (i.e., replacement of vacant breeding positions by dispersing individuals) and reproductive success could be minimized, thus reducing the number of potential breeding groups and average group size and thereby hindering species' recovery. Additionally, proximity to neighboring groups could be particularly important for juvenile females that disperse to avoid inbreeding depression (Daniels and Walters 2000) and for breeding females that disperse to new groups between breeding seasons. Such benefits may offset reduced fledgling production driven by increases in competitive interactions between neighboring groups under high density conditions (Chapter 2).

Use of fine-grained habitat metrics improved our ability to parse relative effects of neighboring group density and habitat structure within RCW home ranges. Many previous studies of foraging RCW resource selection were reliant on coarse stand-level habitat data (e.g., Hardesty et al. 1997, James et al. 1997, 2001, Walters et al. 2002, McKellar et al. 2014). Thus the fine-grained spatial distribution of neighboring groups may help account for relatively large range-wide variation in resource selection by foraging RCWs that raises questions about the generality of range-wide structural thresholds that guide RCW habitat conservation (Garabedian et al. 2014*a*, *b*, McKellar et al. 2014, Hiers et al. 2016). This association of factors receives relatively little focus in the current RCW foraging habitat guidelines (Saenz et al. 2002), which largely are based on explicit structural habitat thresholds derived from stand-level resource selection by foraging RCWs.

High spatial resolution of RCW UDs allowed us to map potential RCW habitat as a continuum of quality that improved precision of potential habitat maps in comparison to current approaches (e.g., the RCW Foraging Matrix Application; USFWS 2005) that produce binary maps of potential habitat. Maps of predicted habitat use based on highly-resolved UDs offer greater potential for targeted within-stand management not offered by recent approaches reliant on stand-level forest structure within arbitrary distance buffers (McKellar et al. 2014). For example, despite significant negative responses of foraging RCWs to hardwood midstory encroachment at fine grains (0.64-ha grains; Garabedian et al. *In prep.*), the current RCW Matrix Habitat Model does not incorporate fine-grained habitat structure or habitat use needed to detect these responses within stands (U.S. Fish and Wildlife Service 2003). Varying grain sizes of individual LiDAR-derived habitat attributes may offer further improvements to model fit, offer insight into the scale at which RCWs respond consistently to specific pine size classes in the species' foraging habitat guidelines, and improve precision of habitat maps (Guisan et al. 2007, Gottschalk et al. 2011, Laforge et al. 2015*b*, *a*). Because selection of pines by foraging RCWs shifts with availability across the species' range (Zwicker and Walters 1999), a multi-grained approach could allow managers to target specific pine size classes at different extents based on local forest structure. For example, on second-growth forests with few isolated relic old-growth pines or otherwise limited distribution of pines ≥35.6 cm dbh across the landscape (e.g., Eglin Air Force Base, Florida; McKellar et al. 2015), it could be more informative to model fine-grained use of large pines that may be used as cavity trees within coarse-grained stand-level BA measures of pines ≥25.4 cm dbh used primarily for foraging. Such information can help managers use limited resources to their fullest potential in RCW habitat conservation as populations continue to grow and require additional acreage of foraging and nesting habitat to support new potential breeding groups (Reed et al. 1988).

Spatial criteria are especially important in development of guidelines for strategic management of neighboring RCW groups in previously unoccupied habitat, particularly under high density conditions. A potential disadvantage from the lack of spatial guidelines in the current USFWS recovery plan is that potential RCW habitat remains unoccupied when it could support additional potential breeding groups that contribute to population recovery. RUF models may be useful for predicting areas of high value to RCWs throughout the Savannah River Site, allowing more precise use of recruitment clusters to facilitate population expansion in unoccupied foraging habitat. Because the Savannah River Site is divided into two distinct subpopulations, establishing recruitment clusters in unoccupied habitat between the two subpopulations requires strategic placement of recruitment clusters to promote connectivity (Saenz et al. 2001, 2002).

Our study highlights the importance of social factors in determining RCW habitat use, potentially due to increased social connectivity and associated benefits to juvenile dispersal in dense aggregations of RCW groups (Azevedo et al. 2000, Kesler et al. 2010, Trainor et al. 2013*a*, Trainor et al. 2013*b*). Additional studies are needed to combine data on social interactions with information on fitness, group composition, and breeder age to gain a broader understanding of how the interplay of habitat and social factors can guide RCW management. This could be especially important in understanding range-wide variation in resource selection, home ranges, and reproductive success (Walters et al. 2002, Garabedian et al. 2014*b*, McKellar et al. 2014, 2015, Williamson et al. 2016). Specifically, placement of recruitment clusters within 200- to 400-m of neighboring RCW foraging partitions would be superior in habitat with $\geq$22 pines $\geq$35.6 cm dbh/ha, $\geq$2.3 m^2/ha BA of pines $\geq$25.4 cm dbh, $<$0.4 m^2/ha BA of hardwoods $<$22.9 cm dbh, and $<$10% hardwood canopy cover could facilitate occupation of recruitment clusters and establishment potential breeding groups in habitat that would not be considered based on current USFWS guidelines. Additional consideration for the distribution and number of neighboring RCW groups will allow managers to prioritize RCW habitat for installation of recruitment clusters based on population density and habitat structure, both of which have important effects on RCW habitat use, but only one of which is integrated into current habitat management guidelines.

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Table 3.1. Definitions of 80- x 80-m resolution covariates used to fit spatially-explicit grid-based resource utilization functions for a sample 44 foraging red-cockaded woodpeckers on the Savannah River Site (n = 34) and Carolina Sandhills National Wildlife Refuge (n = 10), South Carolina, April 2013 and March 2015. Data included high-resolution LiDAR-derived estimates of forest structure and composition (LiDAR habitat thresholds), and multiscale summaries of the number nearest neighboring groups (Knn), number of cavity tree starts (Starts), Euclidian distance to cavity tree cluster (ClusterDist), and the average annual frequency of neighboring group interactions (Intrasp).

Variable type	Variable description
LiDAR habitat thresholds	
Pines $\geq$35.6 cm dbh/ha	$\geq$22 pines/ha that are $\geq$35.6 cm dbh
BA of pines $\geq$25.4 cm dbh	BA $\geq$2.3 m^2/ha of pines $\geq$25.4 cm dbh
Hardwood canopy cover	<10% hardwood canopy cover
BA hardwoods 7.6-22.9 cm dbh	BA <0.4 m^2/ha of hardwoods 7.6-22.9 cm dbh
Knn	
Knn200m	Number of active RCW clusters within 200-m radii
Knn400m	Number of active RCW clusters within 400-m radii
Knn800m	Number of active RCW clusters within 800-m radii
Knn1600m	Number of active RCW clusters within 1600-m radii
Knn2000m	Number of active RCW clusters within 2000-m radii
ClusterDist	
Cluster200m	Distance from cavity tree cluster within 200-m radii
Cluster400m	Distance from cavity tree cluster within 400-m radii
Cluster800m	Distance from cavity tree cluster within 800-m radii
Starts	
Starts200m	Number of cavity tree starts within 200-m radii
Starts400m	Number of cavity tree starts within 400-m radii
Starts600m	Number of cavity tree starts within 600-m radii
Starts800m	Number of cavity tree starts within 800-m radii

Table 3.1. Continued.

Variable type	Variable description
Intrasp	
Intrasp100m	Frequency of intraspecific interactions within 100-m radii
Intrasp200m	Frequency of intraspecific interactions within 200-m radii
Intrasp300m	Frequency of intraspecific interactions within 300-m radii
Intrasp400m	Frequency of intraspecific interactions within 400-m radii

Table 3.2. Spatially-explicit 80- x 80-m resolution covariates used to model variation in utilization distributions across multiple spatial extents (Extent) for a sample of 44 foraging red-cockaded woodpeckers on the Savannah River Site (n = 34) and Carolina Sandhills National Wildlife Refuge (n = 10), South Carolina, between April 2013 and March 2015. Data include the number of nearest neighboring groups (Knn), number of cavity tree starts (Starts), Euclidian distance to cavity tree cluster (ClusterDist), and the average annual frequency of neighboring group interactions (Intrasp).

		Savannah River Site		Carolina Sandhills NWR	
Covariate	Extent	Mean	SD	Mean	SD
Knn	200-m	0.43	0.53	0.41	0.49
	400-m	0.93	0.65	1.11	0.63
	800-m	2.4	1.27	3.64	1.13
	1600-m	7.02	2.42	12.9	2.52
	2000-m	10.12	2.94	18.96	2.46
ClusterDist	200-m	51.06	67.41	52.05	69.81
	400-m	181.55	132.97	179.32	120.61
	800-m	234.35	155.42	242.73	139.24
Starts	200-m	48.24	64.28	53.94	67.36
	400-m	122.34	119.86	148.98	116.12
	600-m	184.45	161.77	188.74	140.21
	800-m	229.51	197.3	244.47	187.2
Intrasp	100-m	12.31	12.43	1.85	2.46
	200-m	7.33	8.63	6.12	5.62
	300-m	3.66	5.13	12.14	8.77
	400-m	1.16	2.24	19.46	11.74

Table 3.3. Comparison of multiscale effects of the number of neighboring red-cockaded woodpecker groups (Knn), frequency of intraspecific interactions (Intra), distance to cavity tree starts, and distance to cavity tree clusters on space use by 44 foraging woodpecker groups on the Savannah River Site (*n* =34) and Carolina Sandhills National Wildlife Refuge (*n* = 10), South Carolina April 2013 and March 2015.

Parameter	Standardized $\bar{\beta}$ (SE)	95% CI		Direction		Frequency Top Model
				+	-	
Knn 200m	36.451 (1.596)	33.807	40.095	38	6	34
Knn 400m	23.480 (0.029)	16.836	24.124	31	13	6
Knn 800m	-0.288 (27.657)	-6.932	6.356	28	16	2
Knn 1600m	0.563 (19.953)	-6.081	7.207	19	25	1
Knn 2000m	3.736 (3.390)	-2.908	10.380	17	27	1
Intra 100m	1.704 (4.505)	-2.371	5.778	26	18	4
Intra 200m	1.534 (7.253)	-2.541	5.608	26	18	6
Intra 300m	1.422 (2.389)	-2.653	5.496	39	5	6
Intra 400m	2.032 (2.079)	-2.043	6.106	40	4	28
Cavity Starts 200m	0.075 (0.001)	0.070	0.081	30	14	26
Cavity Starts 400m	-0.076 (0.001)	-0.081	-0.071	14	30	14
Cavity Starts 600m	-0.109 (0.004)	-0.115	-0.104	18	26	3
Cavity Starts 800m	-0.113 (0.003)	-0.118	-0.107	8	36	1
Cluster Distance 200m	0.181 (0.001)	0.174	0.188	44	0	32
Cluster Distance 400m	-0.063 (0.001)	-0.070	-0.056	20	24	9
Cluster Distance 800m	-0.145 (0.003)	-0.152	-0.138	1	43	3

Table 3.4. Spatially-explicit data used to model red-cockaded woodpecker habitat use within 99% utilization distribution (UD) volume contours for woodpecker groups followed on Savannah River Site, South Carolina, in 2014 (*n* = 34). Data collected during home range surveys include the number of neighboring groups (Knn), number of cavity tree starts (Starts), Euclidian distance to cluster centroids (ClusterDist) each summarized within 200 m of 80- x 80-m UD grid cells, and the number of neighboring group interactions within 400 m of 80- x 80-m UD grid cells (Intrasp). Habitat data include total LiDAR-derived ha of foraging habitat with ≥22 pines ≥35.6 cm dbh/ha (DLP22), ≥2.3 m^2/ha basal area (BA) of pines ≥25.4 cm dbh (BAMP2.3), <0.4 m^2/ha BA of hardwoods 7.6-22.9 cm dbh (BASH0.4), and <10% hardwood canopy cover (HWCC10).

Group	Knn	ClusterDist	Starts	Intrasp	DLP22	BAMP2.3	BASH0.4	HWCC10
22014	0.49	55.1	55.48	0.03	174.08	30.08	112.64	166.4
22022	0.56	66.05	4.64	0.22	195.84	81.28	56.32	173.44
22024	0.34	35.45	59.21	0.06	199.68	124.16	64.64	183.04
24017	0.41	58.57	54.09	0.21	168.96	59.52	58.88	209.28
24024	0.44	50.56	40.21	0.31	175.36	93.44	46.08	184.96
24026	0.40	39.74	0.74	0.35	211.2	124.8	62.72	178.56
24033	0.33	34.33	27.85	0.17	204.8	56.32	37.76	167.04
24035	0.61	64.62	4.56	0.89	199.68	125.44	124.16	183.68
24048	0.41	38.48	63.55	0.1	46.72	58.2	124.16	209.28
25018	0.32	33.68	69.53	0.66	343.04	239.36	224	317.44
25023	0.32	35.79	38.63	0.03	188.16	113.92	73.6	187.52
25043	0.42	41.85	42.68	1.01	334.72	224.64	155.52	360.32
26029	0.36	39.03	45.42	0.33	188.16	85.76	91.52	158.72
26032	0.46	46.83	7.23	0.33	230.4	77.44	190.72	357.12
27002	0.59	66.66	57.42	0.21	359.04	179.84	37.12	225.28
27006	0.32	42.75	34.35	0.32	384.64	387.2	199.68	393.6
27009	0.35	49.56	40.42	0.63	248.96	134.4	34.56	200.32
27014	0.40	35.63	43.95	2.24	354.56	233.6	101.76	252.8
27033	0.34	63.25	0.99	0.38	421.76	443.52	104.96	410.88
27047	0.42	52.07	61.76	0.76	205.44	193.28	32.64	131.84
30002	0.44	49.5	58.06	2.62	420.48	157.44	325.12	430.72
30080	0.54	59.98	46.76	0.82	444.16	309.12	174.72	409.6
80030	0.41	60.68	5.23	0.09	216.32	183.68	87.68	202.88
81022	0.38	46.83	71.61	0.43	229.12	195.2	73.6	150.4
81026	0.49	57.15	10.11	0.32	207.36	90.88	49.92	154.88

Table 3.4. Continued

Group	Knn	ClusterDist	Starts	Intrasp	DLP22	BAMP2.3	BASH0.4	HWCC10
81032	0.20	20.57	47.27	0.25	231.04	228.48	103.04	181.76
81034	0.54	57.04	56.75	1.87	332.8	254.72	157.44	274.56
81036	0.52	57.04	72.16	2.35	385.28	285.44	140.8	364.16
82015	0.44	45.75	68.32	1.38	404.48	389.12	168.32	364.8
82036	0.58	66.14	53.78	1.68	442.24	408.96	406.4	370.56
82044	0.61	55.84	88.42	1.89	395.52	358.4	114.56	361.6
82106	0.51	43.78	57.09	3.42	389.76	332.8	170.88	358.4
82107	0.28	84.15	57.09	1.31	396.16	336	144.64	361.6
82109	0.41	51.14	46.15	1.67	366.72	277.76	225.28	356.48

Table 3.5. Resource utilization function (RUF) candidate models with unstandardized coefficients, 95% confidence intervals for red-cockaded woodpecker utilization distributions (UD) on the Savannah River Site, South Carolina, in 2013 (n = 20). Models were fit with covariates representing LiDAR-derived habitat thresholds (LiDAR) plus covariates for the number nearest neighboring groups (Knn) within 200-m of UD grid cells, frequency of intraspecific interactions within 400-m of UD grid cells (Intraspecific), distance to cavity tree clusters within 200-m of UD grid cells (ClusterDist), and the distribution of cavity tree starts within 200-m of UD grid cells (Starts).

RUF Model	Unstandardized $\bar{\beta}$	95% CI	Frequency Top model
Knn + LiDAR			15
Knn	30.867	14.155, 47.579	
DLP22	5.983	1.407, 5.984	
BAMP2.3	4.835	3.976, 5.695	
BASH0.4	5.956	2.021, 9.892	
HWCC10	11.589	6.85, 16.327	
ClusterDist + LiDAR			3
ClusterDist	-0.123	-0.138, -0.107	
DLP22	2.306	-1.269, 5.882	
BAMP 2.3	2.521	0.033, 5.009	
BASH0.4	6.165	3.101, 9.222	
HWCC10	8.561	5.961, 11.161	
Intraspecific + LiDAR			1
Intraspecific	-0.069	-0.090, -0.048	
DLP22	4.642	-0.874, 9.662	
BAMP2.3	6.969	3.686, 10.434	
BASH0.4	11.194	6.855, 16.352	
HWCC10	15.445	12.041, 17.937	
Starts + LiDAR			1
Starts	-0.1	-0.124, -0.077	
DLP22	0.186	-3.689, 4.062	
BAMP2.3	2.628	0.461, 4.795	
BASH0.4	9.641	6.127, 13.155	
HWCC10	16.007	8.312, 13.044	

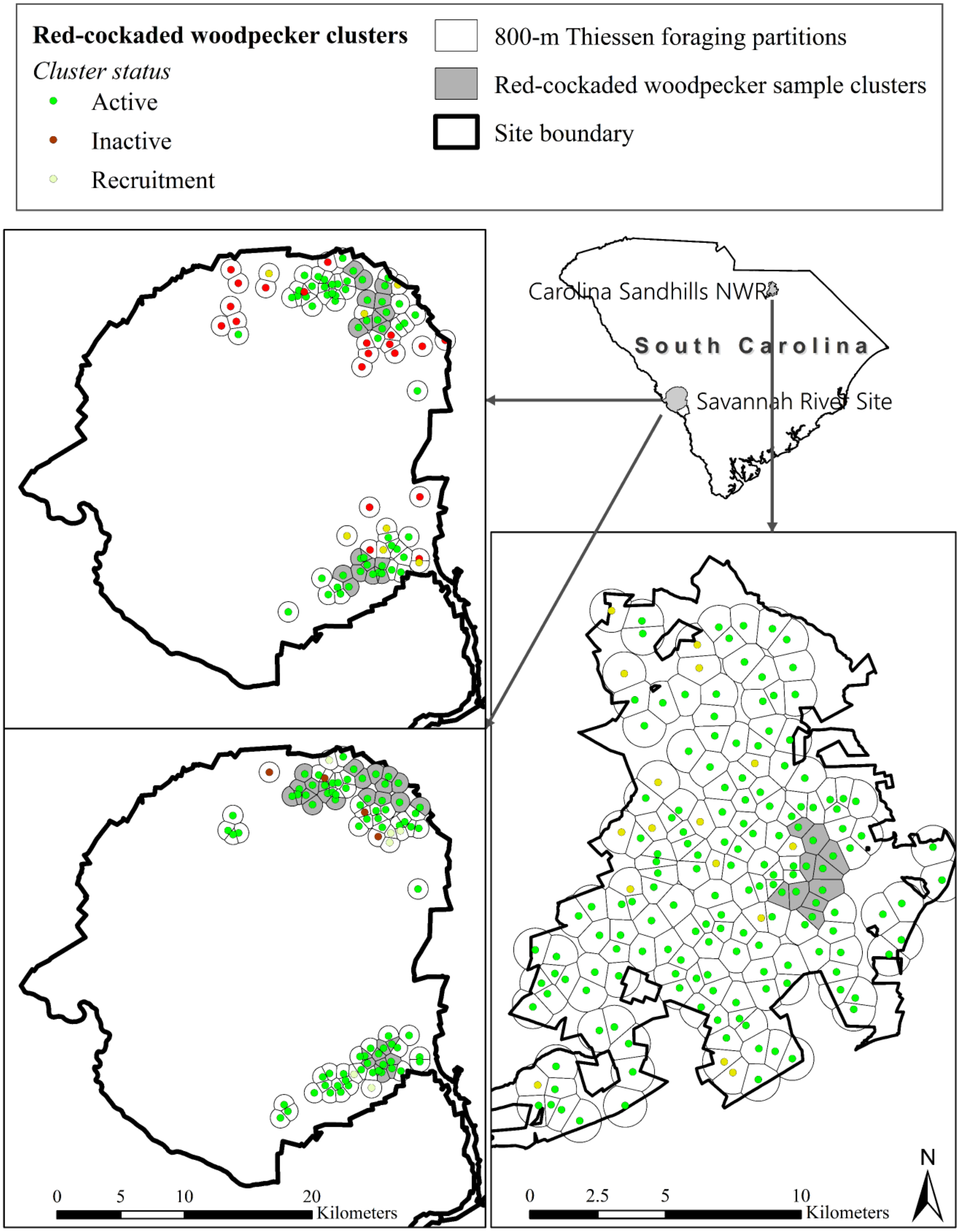

Figure 3.1. The spatial distribution and status of red-cockaded woodpecker cavity tree clusters on Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina, in 2013 and 2014.

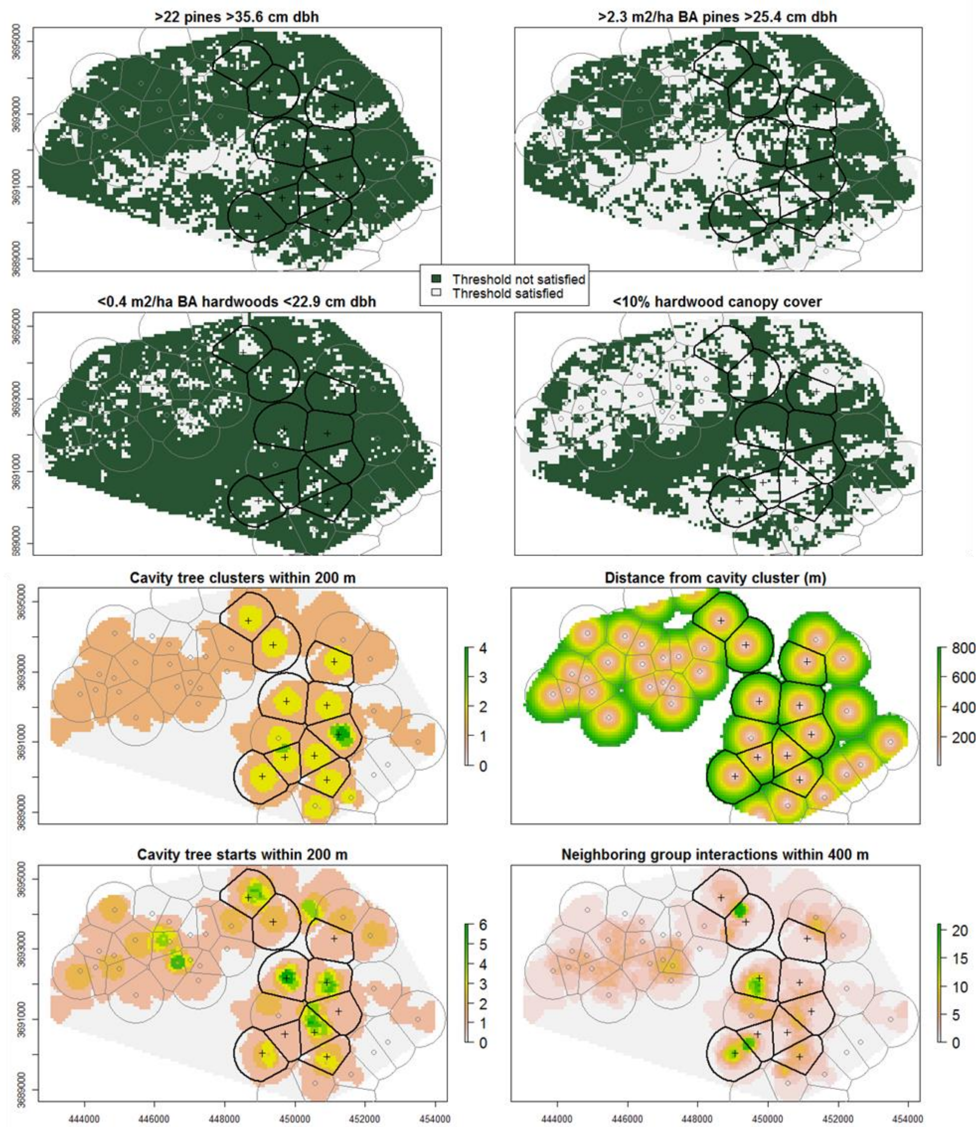

Figure 3.2. Spatially-explicit data used to model variation in red-cockaded woodpecker group habitat use at 80- x 80-m resolution within 99% utilization distribution (UD) volume contours for a sample of 10 groups in the northern subpopulation on the Savannah River Site, South Carolina, in 2013. Data include the spatial distribution and number of neighboring groups within 200 m of UD grid cells, Euclidian distances (m) to cavity tree clusters, number of cavity tree starts within 200 m of UD grid cells, the number of neighboring group interactions within 400 m of UD grid cells, and LiDAR-derived foraging habitat with ≥22 pines ≥35.6 cm dbh/ha, ≥2.3 m^2/ha basal area (BA) of pines ≥25.4 cm dbh, <0.4 m^2/ha BA of hardwoods 7.6-22.9 cm dbh, and <10% hardwood canopy cover. Black and grey polygons delineate 800-m Thiessen foraging partitions for sampled and unsampled woodpecker groups, respecitvely. Black crosses and open circles represent locations of cavity tree clusters for sampled and unsampled groups, respectively.

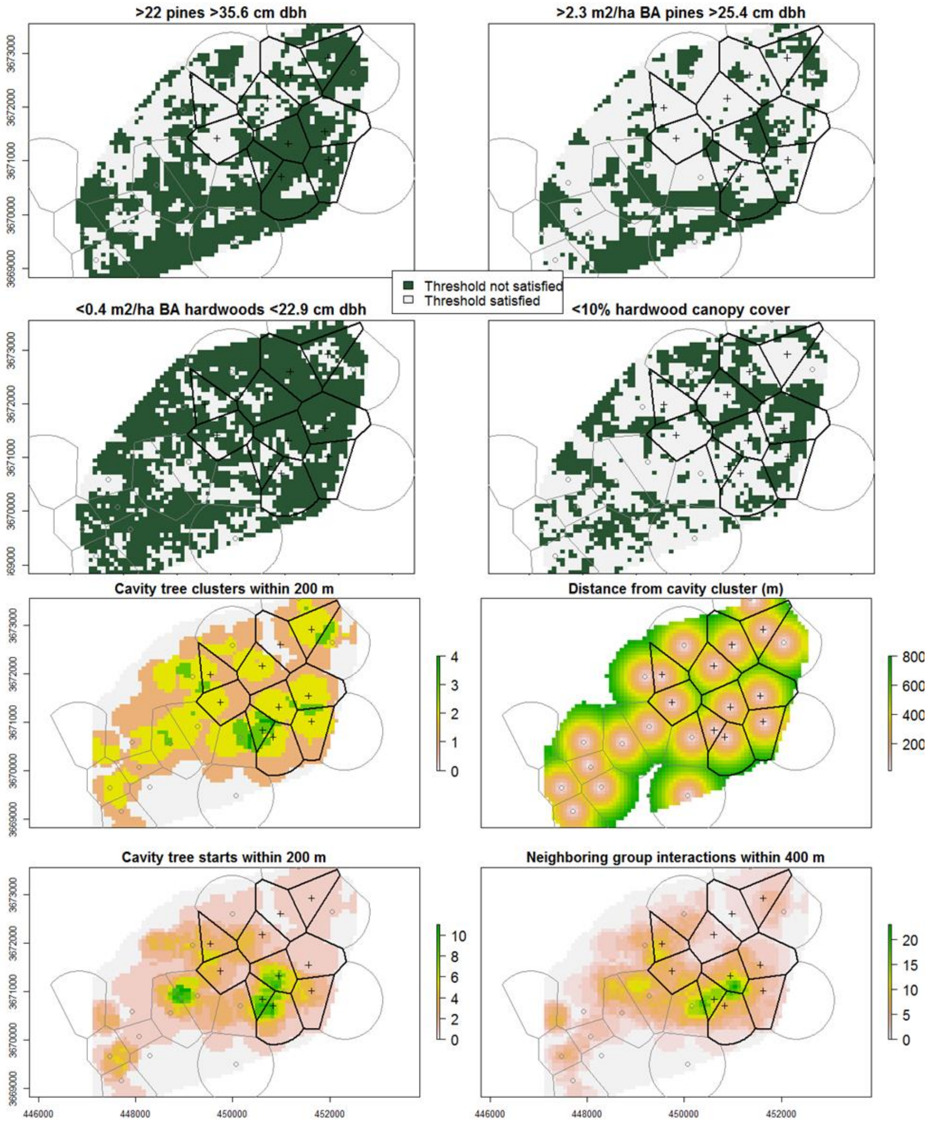

Figure 3.3. Spatially-explicit data used to model variation in red-cockaded woodpecker group habitat use at 80- x 80-m resolution within 99% utilization distribution (UD) volume contours for a sample of 10 woodpecker groups in the southern subpopulation on the Savannah River Site, SC, in 2013. Data include the spatial distribution and number of neighboring groups within 200 m of UD grid cells, Euclidian distances (m) to cavity tree clusters, number of cavity tree starts within 200 m of UD grid cells, the number of neighboring group interactions within 400 m of UD grid cells, and LiDAR-derived foraging habitat with $\geq$22 pines $\geq$35.6 cm dbh/ha, $\geq$2.3 m^2/ha basal area (BA) of pines $\geq$25.4 cm dbh, <0.4 m^2/ha BA of hardwoods 7.6-22.9 cm dbh, and <10% hardwood canopy cover. Black and grey polygons delineate 800-m Thiessen foraging partitions for sampled and unsampled woodpecker groups, respecitvely. Black crosses and open circles represent locations of cavity tree clusters for sampled and unsampled groups, respectively.

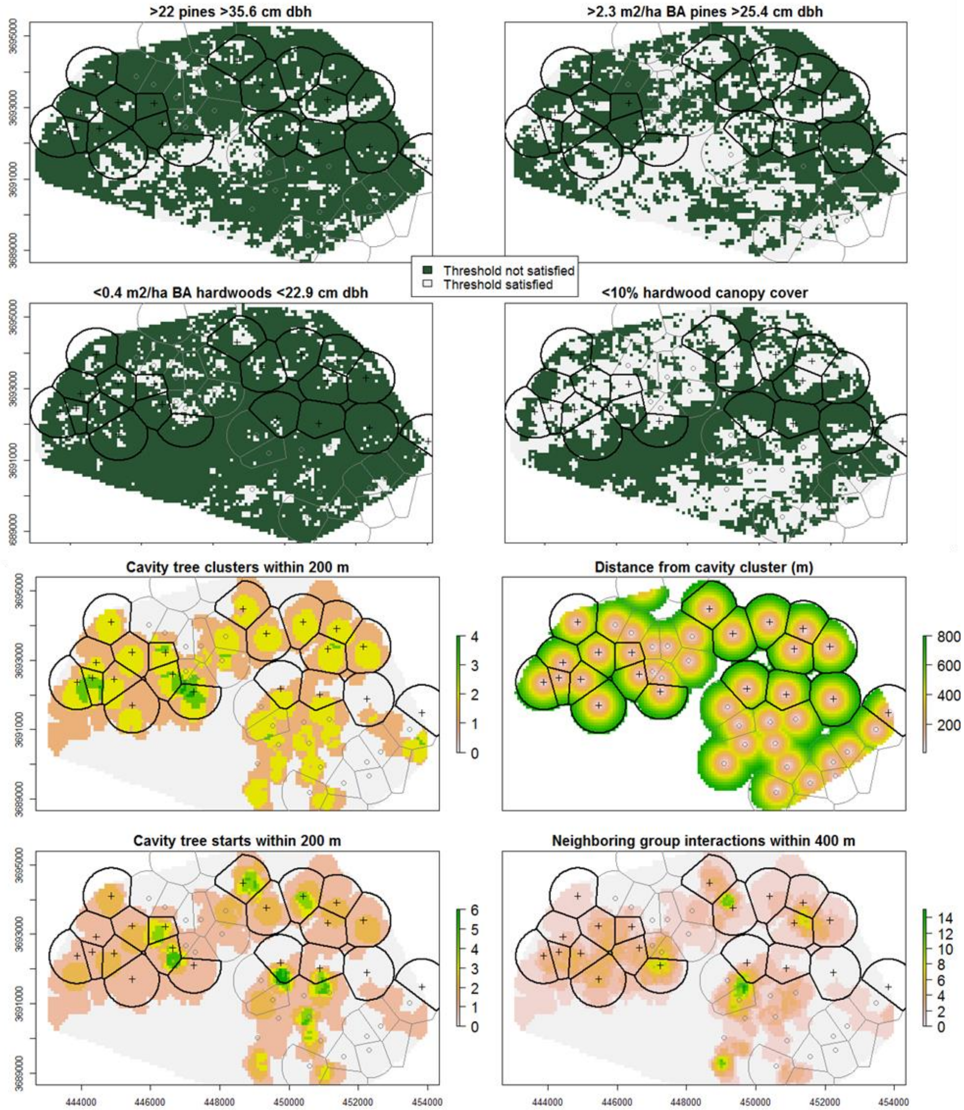

Figure 3.4. Spatially-explicit data used to model variation in red-cockaded woodpecker group habitat use at 80- x 80-m resolution within 99% utilization distribution (UD) volume contours for 20 woodpecker groups in the northern subpopulation on the Savannah River Site, South Carolina, in 2014. Data include the spatial distribution and number of neighboring groups within 200 m of UD grid cells, Euclidian distances (m) to cavity tree clusters, number of cavity tree starts within 200 m of UD grid cells, the number of neighboring group interactions within 400 m of UD grid cells, and LiDAR-derived foraging habitat with $\geq$22 pines $\geq$35.6 cm dbh/ha, $\geq$2.3 m^2/ha basal area (BA) of pines $\geq$25.4 cm dbh, <0.4 m^2/ha BA of hardwoods 7.6-22.9 cm dbh, and <10% hardwood canopy cover. Black and grey polygons delineate 800-m Thiessen foraging partitions for sampled and unsampled woodpecker groups, respecitvely. Black crosses and open circles represent locations of cavity tree clusters for sampled and unsampled groups, respectively.

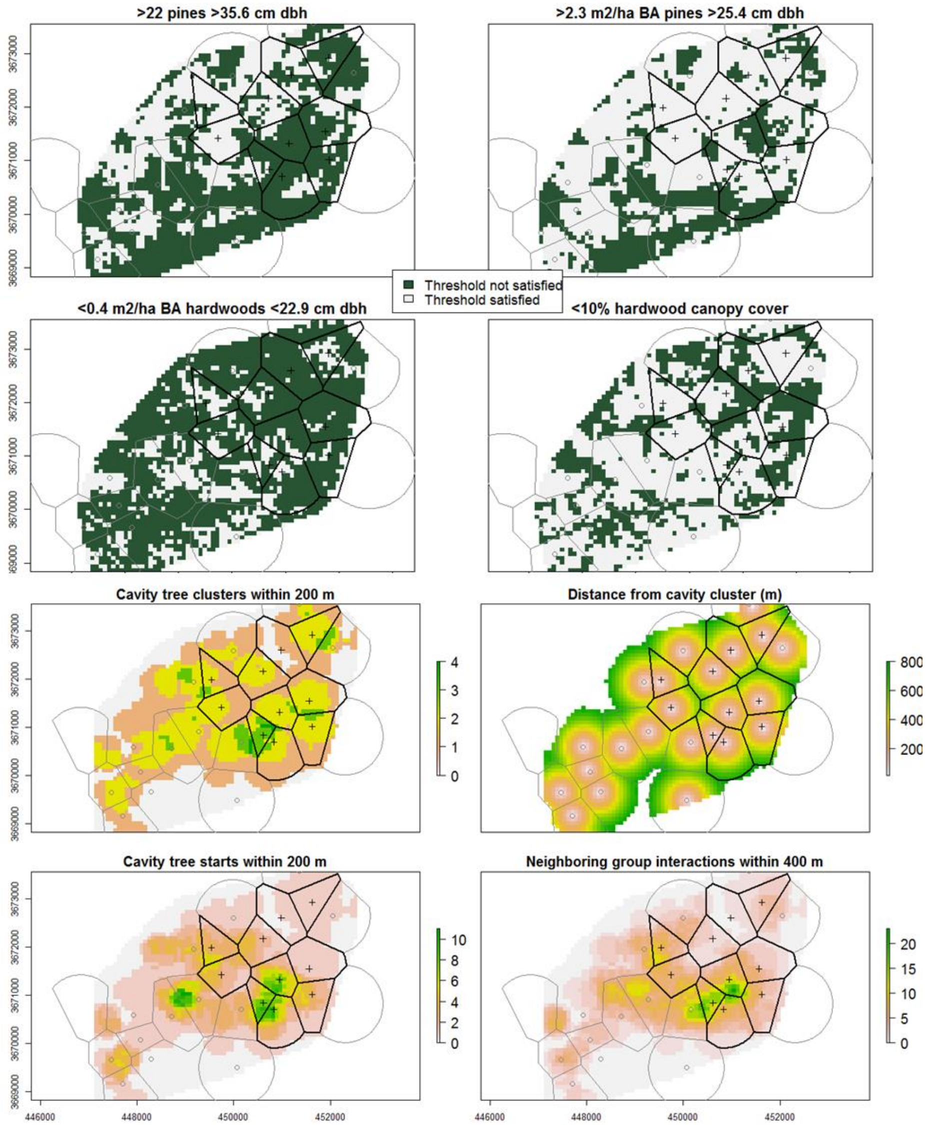

Figure 3.5. Spatially-explicit data used to model variation in red-cockaded woodpecker group habitat use at 80- x 80-m resolution within 99% utilization distribution (UD) volume contours for a sample of 10 woodpecker groups in the southern subpopulation on the Savannah River Site, South Carolina, in 2014. Data include the spatial distribution and number of neighboring groups within 200 m of UD grid cells, Euclidian distances (m) to cavity tree clusters, number of cavity tree starts within 200 m of UD grid cells, the number of neighboring group interactions within 400 m of UD grid cells, and LiDAR-derived foraging habitat with $\geq$22 pines $\geq$35.6 cm dbh/ha, $\geq$2.3 m^2/ha basal area (BA) of pines $\geq$25.4 cm dbh, <0.4 m^2/ha BA of hardwoods 7.6-22.9 cm dbh, and <10% hardwood canopy cover. Black and grey polygons delineate 800-m Thiessen foraging partitions for sampled and unsampled woodpecker groups, respecitvely. Black crosses and open circles represent locations of cavity tree clusters for sampled and unsampled groups, respectively.

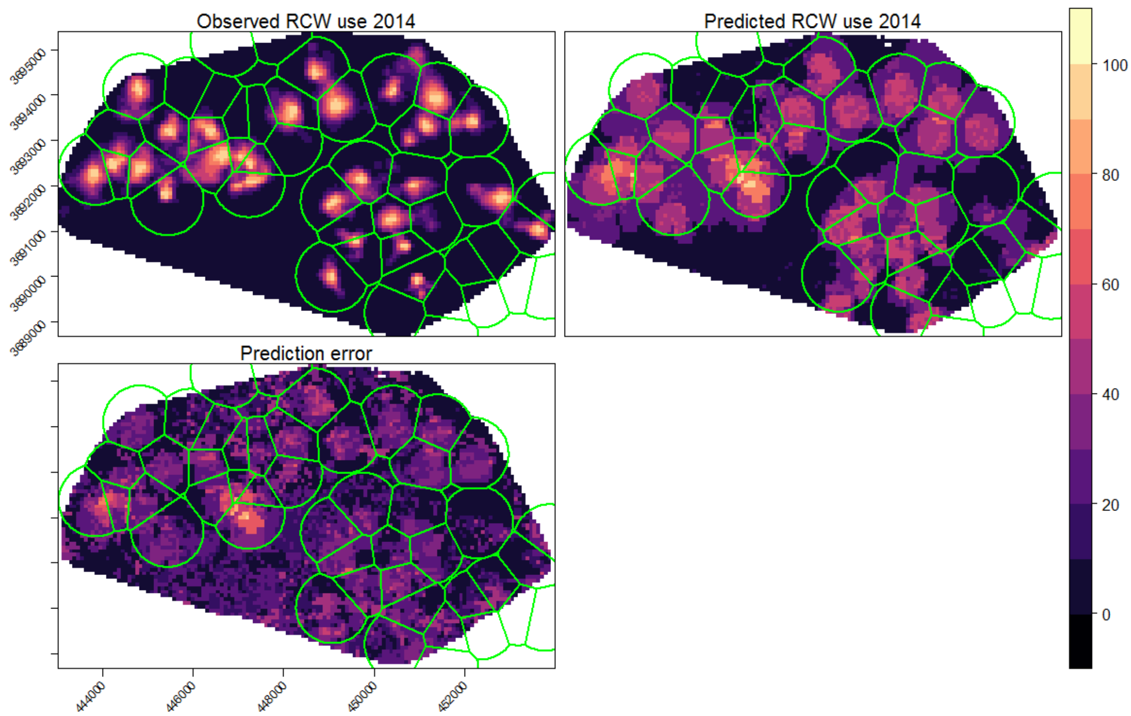

Figure 3.6. Spatial projections of predicted habitat use by 24 foraging red-cockaded woodpecker groups in the northern subpopulation on the Savannah River Site in 2014. Color ramps reflect the probability of use for the observed utilization distributions (UD) for foraging woodpecker groups in 2014 (top left panel), predicted use by foraging woodpecker groups in 2014 (top right), and prediction error (bottom left panel) based on the number of neighboring groups within 200 m of 80 x 80 m UD grid cells and LiDAR-derived habitat with $\geq$22 cm dbh/ha pines $\geq$35.6 cm dbh/ha, $\geq$2.3 m^2/ha basal area (BA) of pines $\geq$25.4 cm dbh, <0.4 m^2/ha BA of hardwoods <22.9 cm dbh/ha, and <10% hardwood canopy cover. Green polygons delineate 800-m Thiessen foraging partitions for individual woodpecker groups.

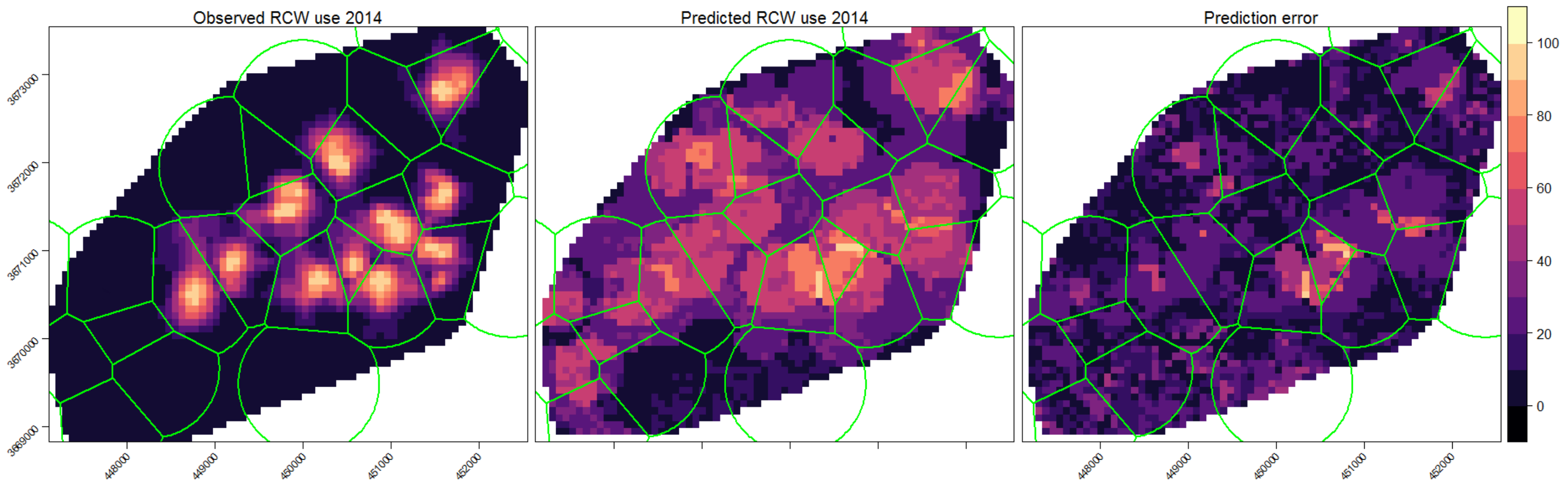

Figure 3.7. Spatial projections of predicted habitat use by 10 foraging red-cockaded woodpecker groups in the southern subpopulation on the Savannah River Site in 2014. Color ramps reflect the probability of use for observed utilization distributions (UD) for foraging woodpecker groups in 2014 (left panel), predicted use by foraging woodpecker groups in 2014 (middle panel), and prediction error (right panel) based on the number of neighboring groups within 200 m of 80- x 80-m UD grid cells and LiDAR-derived habitat with $\geq$22 cm dbh/ha pines $\geq$35.6 cm dbh/ha, $\geq$2.3 m^2/ha basal area (BA) of pines $\geq$25.4 cm dbh, <0.4 m^2/ha BA of hardwoods <22.9 cm dbh/ha, and <10% hardwood canopy cover. Green polygons delineate 800-m Thiessen foraging partitions for individual woodpecker groups.