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Use of LiDAR to define habitat thresholds for forest bird conservation

James E. Garabedian [a,*], Christopher E. Moorman [a], M. Nils Peterson [a], John C. Kilgo [b]

[a] Fisheries, Wildlife and Conservation Biology Program, North Carolina State University, Box 7646, Raleigh, NC 27695, USA
[b] Southern Research Station, USDA Forest Service, Savannah River, P.O. Box 700, New Ellenton, SC 29809, USA

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ABSTRACT

Quantifying species-habitat relationships provides guidance for establishment of recovery standards for endangered species, but research on forest bird habitat has been limited by availability of fine-grained forest structure data across broad extents. New tools for collection of data on forest bird response to fine-grained forest structure provide opportunities to evaluate habitat thresholds for forest 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-h period twice per month between April 2013 and March 2015. Next, we used piecewise regression to characterize RCW threshold responses to 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. We identified lower and upper thresholds for densities of pines ≥35.6 cm dbh (22, 65 trees/ha), basal area (BA) of pines ≥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 ≥25.4 cm dbh (β = 0.055, 95% CI = 0.022–0.087), and ≥22 pines ≥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. Selection ranks prioritized multiple thresholds below USFWS range-wide recovery thresholds, indicating site-specific management goals may be beneficial for RCW conservation. Fine-grained LiDAR-derived habitat data coupled with GPS-derived habitat use can guide forest bird conservation by identifying the full range of structural conditions associated with threshold responses.

1. 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). Habitat conditions (e.g., vegetation composition or structure) where resource use is high relative to 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 (Berl et al., 2015; Hernández et al., 2006).

Resource selection functions (Manly et al., 2007) have benefited forest 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 relative to 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), and patch size (Collier et al., 2012; Dudley et al., 2012). These quantitative thresholds in turn serve as conservation targets to maximize species'

* Corresponding author at: Department of Forestry and Environmental Resources, North Carolina State University, Box 7646, Raleigh, NC 27695, USA.
E-mail address: jegarabe@ncsu.edu (J.E. Garabedian).

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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 (Evans et al., 2014; Suchant et al., 2003). 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 potential impacts of timber harvest on minimum requirements in nesting habitat structure (Poulin et al., 2008). Habitat thresholds have guided conservation of other forest birds, including Eurasian treecreepers (*C. familiaris*; Suorsa et al., 2005), white-browed treecreepers (*Climacteris affinis*; Radford and Bennett, 2004), Bachman's sparrows (*Aimophila aestivalis*; Allen and Burt, 2014), olive-sided flycatchers (*Contopus cooperi*; Robertson, 2012), and several woodpeckers (*Dendrocopus* spp., *Melanerpes* spp., *Picoides* spp., *Picus* spp.; Berl et al., 2015; Bütler et al., 2004; Müller and Bütler, 2010; Roberge et al., 2008; Touihri et al., 2014).

There are practical challenges in deriving habitat thresholds for conservation of species that respond to fine-grained variation in forest structure (Berl et al., 2015; Müller and Bütler, 2010). 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 et al., 2004). 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 forest birds (Swift and Hannon, 2010). 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, 2015). 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 (Cunningham and Johnson, 2012).

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 forest 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 that 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 forest birds, including red-naped sapsuckers (Holbrook et al., 2015), black-throated blue warblers (Goetz et al., 2010), and brown creepers (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). 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; Anich et al., 2012; Roberge et al., 2008).

Conservation of the federally endangered red-cockaded woodpecker (*Leuconotopicus borealis*; RCW) would benefit from research on structural thresholds that define foraging habitat quality (U.S. Fish and Wildlife Service [USFWS], 2003, 1970). 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 (Conner and Rudolph, 1989; Ligon et al., 1986; Walters et al., 2002). As nesting constraints are now mitigated using techniques such as prescribed burning and artificial cavity construction (Allen, 1991; Copeyon, 1990), a better understanding of factors contributing to foraging habitat quality has gained importance in the recovery of this species (USFWS, 2003; Walters et al., 2002). Foraging RCWs consistently exhibit a range-wide preference for the largest and oldest available pines (Engstrom and Sanders, 1997; Porter and Labisky, 1986; Walters et al., 2002; Zwicker and Walters, 1999). 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 (Garabedian et al., 2014b; 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., 2014b). Spadgenske et al. (2004) 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. (2014a) 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 define 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.

2. Materials and methods

2.1. 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 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 2832 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.

2.2. 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 (Fig. 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 (Khan and Walters, 2002; Walters, 1990). Fledgling production data were averaged using observations from 2009 to 2013. Group size data were averaged using observations from 2010 to 2013 because data from 2009 were unavailable.

2.3. Home-range surveys

We followed the sample of 30 foraging RCW groups minimally over a 4-h 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 the location fixes, observers documented basic behaviors (e.g., foraging, resting, cavity work, feeding nestlings, or interspecific interaction) for the breeding male of each group at each 15-min interval. Because our analysis focused on resource selection by foraging RCWs, we used only foraging relocations of breeding males in subsequent analyses.

2.4. LiDAR-derived habitat data

We used high-resolution spatially-explicit LiDAR-derived estimates of forest structure to quantify the amount and condition of foraging habitat available to individual RCW groups. High density (average of 10 returns m^{-2}) airborne LiDAR data used in this study were acquired across the Savannah River Site in February and March 2009 using two Leica ALS50-II laser scanners mounted in separate fixed-wing aircraft (Woolpert, 2009). The FUSION program was used to process and summarize LiDAR sensor data for subsequent analysis (McGaughey, 2009). Point data reduction methods and quality assurance analysis details were provided by Reutebuch and McGaughey (2012).

We used circular, fixed-area plots to collect field vegetation data on 194 ground calibration plots located throughout the Savannah River Site across a range of forest conditions in the spring of 2009. For each plot, we measured forest structural attributes included in the USFWS range-wide foraging habitat guidelines, including live BA and density of pine trees that were ≥35.6, 25.4–35.6, and 7.6–25.4 cm dbh, and for live hardwoods 7.6–22.9 cm dbh. Next, we used regression methods to relate LiDAR sensor data to forest inventory attributes measured on ground calibration plots. We used the resulting regression models to predict detailed and interrelated forest structural attributes included in the USFWS foraging habitat guidelines and subsequently populate raster layers at 20-m resolution with these attributes for all of the Savannah River Site. Finally, we quantified the error in model predictions averaged over several aggregate sizes (i.e., grain size) to identify the grain size that reduced prediction error while maintaining a biologically meaningful grain size. Based on the error associated with model predictions, we selected 0.64 ha as the grain size for our analyses (Garabedian et al., 2014a). 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. (2014a).

2.5. 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.,

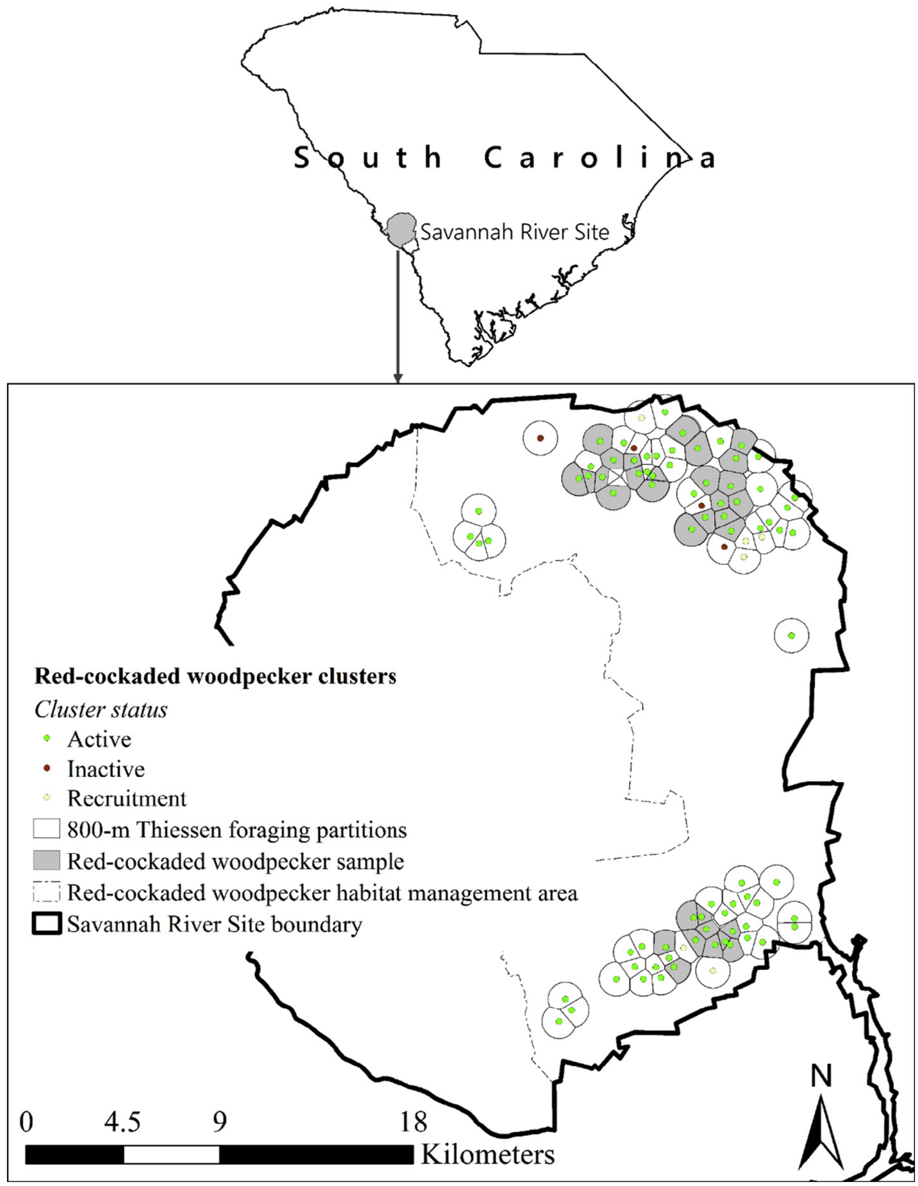

Fig. 1. The spatial distribution and status of red-cockaded woodpecker cavity tree clusters on Savannah River Site, South Carolina, in 2013.

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. We analyzed RCW locations and estimated UDs in the R statistical environment (R Development Core Team, 2015) using the contributed packages "sp" (Bivand et al., 2013; Pebesma and Bivand, 2005) and "adehabitatHR" (Calenge, 2006).

2.6. Threshold analysis

We used piecewise regression to model thresholds 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; Yin et al., 2017).

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 piecewise 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 breakpoint estimates 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

Table 1
Average clutch size, nestling production, fledgling production, and group size reported from previous research across the range of the red-cockaded woodpecker.

Source	Location	Clutch size (SD)	Nestling production (SD)	Fledgling production (SD)	Group size (SD)
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)
Wigley 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 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[a]	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.

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 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 ≥ 5 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).

2.7. 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 to account for the spatial autocorrelation of UD volumes among adjacent 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

Table 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 to 0.034
$x > 65$	22.550	−0.174 (0.037)	−0.247 to −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 to −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 to −0.021
$x > 400$	9.084	−0.003 (0.003)	−0.008 to 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 to −9.973
$0.4 < x < 6.1$	11.760	−1.341 (0.164)	−1.662 to −1.02
$x > 6.1$	6.957	−0.441 (0.267)	−0.965 to 0.083
Hardwood canopy cover/ha (%)			
$x < 6$	18.700	−1.245 (0.14)	−1.520 to −0.970
$6 < x < 31$	12.290	−0.245 (0.032)	−0.307 to −0.183
$x > 31$	5.758	−0.049 (0.051)	−0.148 to 0.050

Table 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

each RCW group UD and set the smoothness of each UD surface to 1.5. We fit RUFs in the R statistical environment (R Development Core Team, 2015) using the contributed package "ruf" (Handcock, 2015).

2.8. 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., 2004). 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).

3. Results

3.1. Woodpecker data

Overall means of reproductive success metrics at the Savannah River Site were within the range of those reported in previous

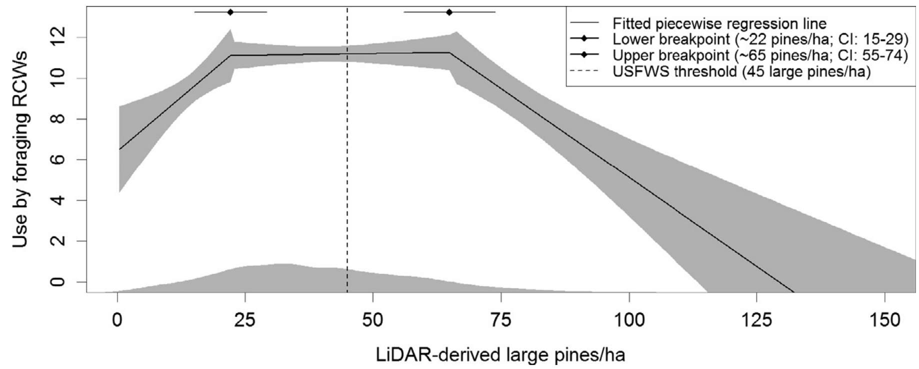

Fig. 2. Fitted piecewise regression model, breakpoints, and 95% confidence intervals (shaded area around fitted line) in resource use by foraging red-cockaded woodpecker groups (n = 30) relative to LiDAR-derived density of pines ≥35.6 cm dbh/ha on Savannah River Site, South Carolina, between April 2013 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.

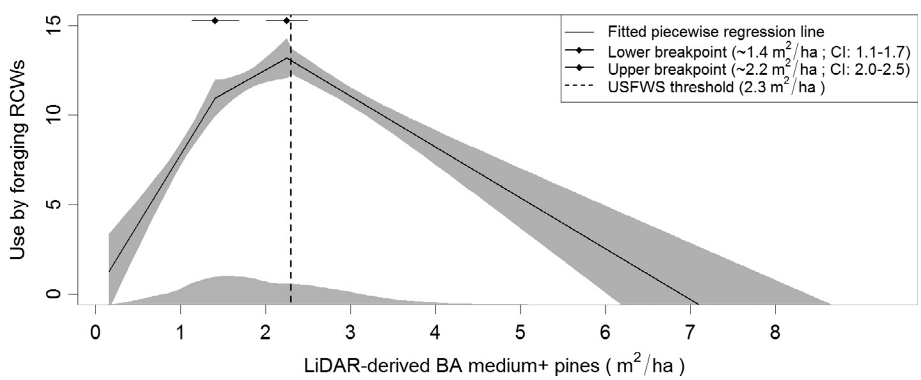

Fig. 3. Fitted piecewise regression model, breakpoints, and 95% confidence intervals (shaded area around fitted line) in resource use by foraging red-cockaded woodpecker groups (n = 30) relative to LiDAR-derived basal area (BA; m^2/ha) of pines ≥25.4 cm dbh on Savannah River Site, South Carolina, between 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.

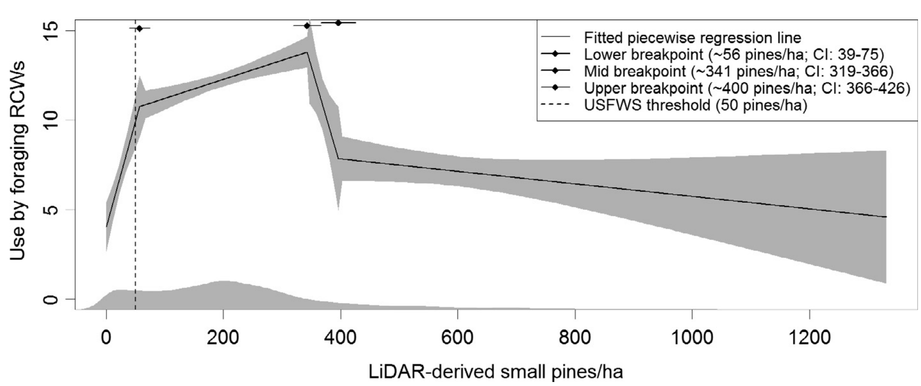

Fig. 4. Fitted piecewise regression model, breakpoints, and 95% confidence intervals (shaded area around fitted line) in resource use by foraging red-cockaded woodpecker groups (n = 30) relative to LiDAR-derived density of pines 7.6–25.4 cm dbh/ha on Savannah River Site, South Carolina, between April 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.

studies (Table 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 2000 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 to 126 m. The total area available to RCWs within boundaries of 99% UD volume contours averaged 135 ha and ranged from 48 to 304 ha.

3.2. Threshold analysis

The most parsimonious piecewise regressions identified breakpoints in use at lower and upper values for density of pines ≥35.6 cm dbh (22, 65 trees/ha), BA of pines ≥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 2). Habitat use by foraging RCWs relative to density of pines ≥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 3). Habitat use relative to BA of pines ≥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 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 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 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 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 4; Figs. 2–6).

3.3. 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 5). Overall, we detected selection of habitat related to thresholds in density of pines ≥35.6 cm dbh/ha, BA of pines ≥25.4 cm dbh, BA of hardwoods 7.6–22.9 cm dbh, and percent hardwood canopy cover (Table 5). The magnitude of selection and ranked importance of each habitat attribute varied among models (Table 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 ≥2.3 m^2/ha BA of pines ≥25.4 cm dbh, and selection for habitat with <30% hardwood canopy cover (Table 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 ≥1.4 m^2/ha BA of pines ≥25.4 cm dbh, and selection for habitat with ≥22 pines ≥35.6 cm dbh/ha (Table 5). In the models based on upper piecewise regression breakpoints, we did not detect selection or avoidance of habitat satisfying threshold requirements (Table 5).

3.4. 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 6). The regression model accounted for approximately 43% of variation in fledgling production ($F_{6,22}$ = 4.471, p = 0.004). Selection of habitat with <65 pines ≥35.6 cm dbh/ha and RCW group size had significant negative and positive effects on fledgling production, respectively (Table 6). There was moderate agreement between observed fledg-

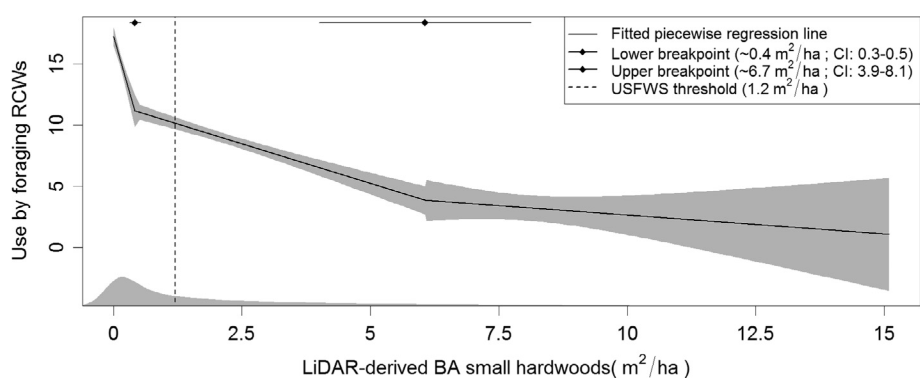

Fig. 5. Fitted piecewise regression model, breakpoints, and 95% confidence intervals (shaded area around fitted line) in resource use by foraging red-cockaded woodpecker groups (n = 30) relative to LiDAR-derived basal area (BA; m^2/ha) of hardwoods 7.6–22.9 cm dbh on Savannah River Site, South Carolina, 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.

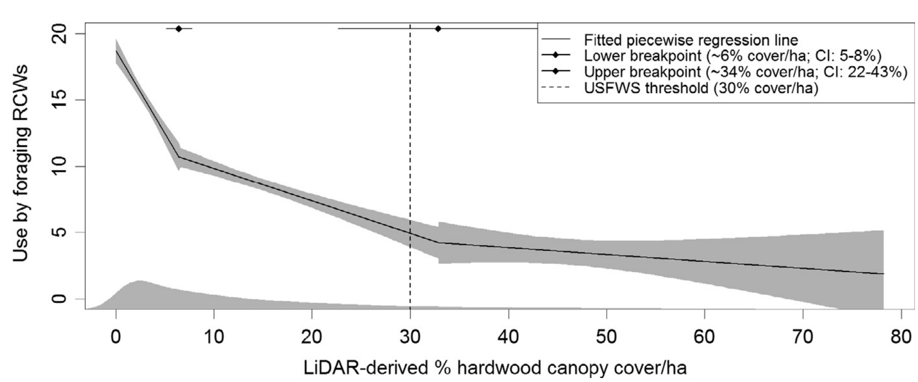

Fig. 6. Fitted piecewise regression model, breakpoints, and 95% confidence intervals (shaded area around fitted line) in resource use by foraging red-cockaded woodpecker groups (n = 30) by foraging RCWs relative to LiDAR-derived percent hardwood canopy cover on Savannah River Site, South Carolina, between 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.

Table 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 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. 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

ling production in 2015 and that predicted by the fitted regression model for 5-year mean fledgling production (Fig. 7).

4. Discussion

Our findings indicate 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 of management for conditions above or below

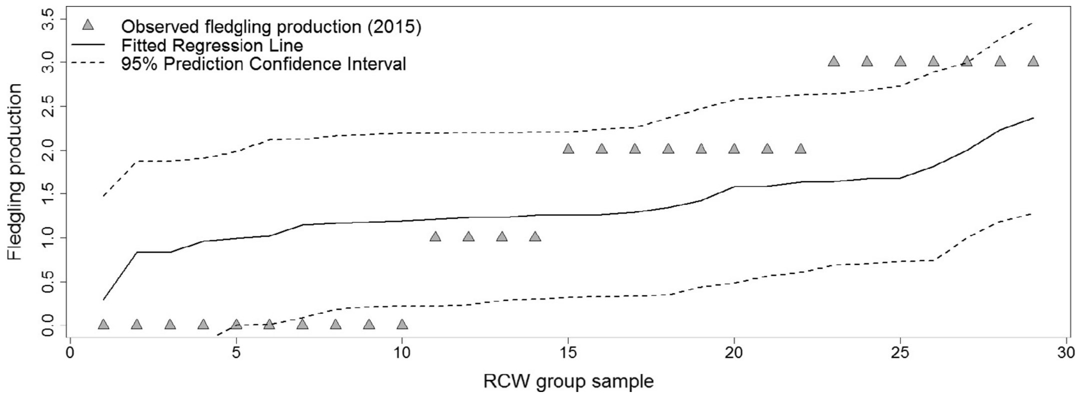

Fig. 7. Prediction confidence intervals for multiple linear regression modeling 5-year mean (2009–2013) fledgling production in response to selection of LiDAR-derived habitat thresholds and group size for red-cockaded woodpecker groups ($n = 30$) on Savannah River Site, South Carolina. Habitat thresholds 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. Gray triangles represent observations of fledgling production by the same sample of 30 woodpecker groups in 2015.

threshold requirements. We provide empirical support for previous assertions that the benefits of large pines are diminished at higher tree densities (e.g., McKellar et al., 2014; Walters et al., 2002), which is particularly important for RCW conservation given the priority to retain the largest and oldest pines across the landscape. Although 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 ≥ 5.6 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 (Hooper, 1996; Smith, 1955). 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 (Graveland and Van Gijzen, 1994; James et al., 1997; Palik et al., 1997; Taylor, 1986). 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. (2016) 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 nonlinear change 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, 2016). 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. Some studies suggest habitat threshold requirements for forest bird reproduction can be more restrictive than threshold requirements for species' presence (Angelstam, 2004; Bütler et al., 2004; Poulin et al., 2008; Roberge et al., 2008). 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).

Applying our approach to identify threshold responses to forest attributes will provide greater management flexibility for recovering endangered species, and managing for other ecosystem services. Forest bird species in addition to the RCW exhibit threshold responses to forest attributes (e.g., brown creepers, Guénette and Villard, 2005; red-headed woodpeckers, [*M. erythrocephalus*]; Berl et al., 2015). Identifying upper and lower thresholds in habitat (Toms and Villard, 2015; Yin et al., 2017) allows managers to consider the widest possible range of acceptable forest attributes, which in turn creates options for achieving multiple objectives (e.g., timber production) on the same landscape (Hiers et al., 2016). For example, in the fire-maintained pine forests of the southeastern United States, lower threshold requirements for pine basal area in RCW foraging habitat may overlap with upper habitat thresholds identified for Bachman's sparrow (Taillie et al., 2015), northern bobwhite (*Colinus virginianus*; Janke and Gates, 2013; Janke et al., 2015), or wild Turkey (*Meleagris gallopavo*; Little et al., 2016).

5. Conclusions

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 ≥35.6 cm dbh from ≥45 pines/ha to ≥22 pines/ha, while continuing to maintain the largest and oldest pines in RCW foraging habitat; (2) reducing the minimum requirements for BA of pines ≥25.4 cm dbh to ≥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 ≥35.6 and ≥25.4 cm dbh into a single metric describing densities of all pines ≥25.4 cm dbh until pines ≥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 ≥25.4 cm dbh ≥1.4 m^2/ha; (2) hardwood midstory BA <1.2 m^2/ha; (3) ≥22 pines ≥35.6 cm dbh/ha; and (4) <400 pines <25.4 cm dbh/ha.

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