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Source: The Condor, 120(2):305-318.
Published By: American Ornithological Society
https://doi.org/10.1650/CONDOR-17-211.1
URL: http://www.bioone.org/doi/full/10.1650/CONDOR-17-211.1

THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 120, 2018, pp. 305–318
DOI: 10.1650/CONDOR-17-211.1

RESEARCH ARTICLE

Relative importance of social factors, conspecific density, and forest structure on space use by the endangered Red-cockaded Woodpecker: A new consideration for habitat restoration

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Submitted October 14, 2017; Accepted December 20, 2017; Published March 14, 2018

ABSTRACT

Understanding how the interplay between social behaviors and habitat structure influences space use is important for conservation of birds in restored habitat. We integrated fine-grained LiDAR-derived habitat data, spatial distribution of cavity trees, and spatially explicit behavioral observations in a multi-scale model to determine the relative importance of conspecific density, intraspecific interactions, and the distribution of cavities on space use by Red-cockaded Woodpeckers (*Picoides borealis*) on 2 sites in South Carolina, USA. We evaluated candidate models using information theoretic methods. Top scale-specific models included effects of conspecific density and number of cavity tree starts within 200 m of Red-cockaded Woodpecker foraging locations, and effects of the number of intraspecific interactions within 400 m of Red-cockaded Woodpecker foraging locations. The top multi-scale model for 22 of 34 Red-cockaded Woodpecker groups included covariates for the number of groups within 200 m of foraging locations and LiDAR-derived habitat with moderate densities of large pines (*Pinus* spp.) and minimal hardwood overstory. These results indicate distribution of neighboring groups was the most important predictor of space use once a minimal set of structural habitat thresholds was reached, and that placing recruitment clusters as little as 400 m from foraging partitions of neighboring groups may promote establishment of new breeding groups in unoccupied habitat. The presence of neighboring groups likely provides cues to foraging Red-cockaded Woodpeckers that facilitate prospecting prior to juvenile dispersal and, to a lesser extent, indicates high-quality forage resources. Careful consideration of local distribution of neighboring groups in potential habitat may improve managers' ability to increase Red-cockaded Woodpecker density on restored landscapes and mitigate isolation of Red-cockaded Woodpecker groups, a problem that negatively affects fitness across the species' range.

Keywords: behaviors, cavity trees, conspecific density, endangered species, LiDAR, multi-scale, Red-cockaded Woodpecker

Importancia relativa de factores sociales, densidad co-específica y estructura del bosque en el uso del espacio por parte de la especie en peligro *Picoides borealis*: Una nueva consideración para la restauración del hábitat

RESUMEN

Entender cómo la interacción entre los comportamientos sociales y la estructura del hábitat influencian el uso del espacio es importante para la conservación de las aves en los hábitats restaurados. Integramos datos de hábitat de grano fino derivados de LiDAR, la distribución espacial de árboles con cavidades y observaciones de comportamiento espacialmente explicitas en un modelo multi-escalar para determinar la importancia relativa de la densidad de individuos co-específicos, de las interacciones intra-específicas y de la distribución de cavidades en el uso del espacio por parte de *Picoides borealis* en dos sitios en Carolina del Sur, EEUU. Evaluamos los posibles modelos usando métodos teóricos de información. Los principales modelos de escala específica incluyeron los efectos de la densidad de individuos co-específicos y del número de árboles con cavidades dentro de los 200 m de las ubicaciones de forrajeo de *P. borealis*, y los efectos del número de interacciones intra-específicas dentro de los 400 m de las ubicaciones de forrajeo de *P. borealis*. El principal modelo de escala específica para 22 de los 34 grupos de *P. borealis* incluyó covariables para el número de grupos dentro de los 200 m de las ubicaciones de forrajeo y el hábitat derivado a partir de LiDAR con densidades moderadas de pinos grandes (*Pinus* spp.) y dosel mínimo de maderas duras. Estos resultados indican que la distribución de los grupos vecinos fue el predictor más importante del uso del espacio una vez que se alcanzó un conjunto mínimo de umbrales de estructura de hábitat, y que la ubicación de clústeres de reclutamiento a tan solo 400 m de las particiones de forrajeo de los grupos vecinos puede promover el establecimiento de nuevos grupos reproductivos en el hábitat desocupado. La presencia de grupos vecinos probablemente le brinda pistas a los individuos de *P. borealis* que forrajean facilitándoles la prospección del hábitat antes de la dispersión de los juveniles y, en menor medida, indica la presencia de recursos forrajeros de alta calidad. Considerar cuidadosamente de la distribución local de los grupos vecinos en el hábitat potencial puede mejorar la capacidad de los gestores de aumentar la densidad de *P. borealis* en los paisajes restaurados y mitigar el aislamiento de los grupos de *P. borealis*, un problema que afecta negativamente la adecuación biológica a través del rango de la especie.

Palabras clave: árboles con cavidades, comportamientos, densidad de individuos co-específicos, especie en peligro, LiDAR, multi-escalar, *P. borealis*

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 critical habitat (Austin 2002).

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 (Ficetola et al. 2014, He et al. 2015). Light distance and ranging (LiDAR) technology has become an invaluable tool for modeling and mapping habitat structure across broad extents while retaining fine-grained 3-dimensional detail (Vierling et al. 2008, 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 (Farrell et al. 2013, Garabedian et al. 2014a). 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, Smart et al. 2012, 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).

High-resolution animal location data have fostered new opportunities to link bird space use to spatially explicit resources using animal utilization distributions (UDs; Worton 1989). 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 scales (Millspaugh et al. 2006, McGarigal et al. 2016). For example, modeling variation in UDs has been used to inform endangered species management by identifying the scale at which species' response to a specific feature is strongest (Campioni et al. 2013). Additionally, identifying the most intensively used areas within UDs may elucidate features most limiting to species that maintain all-purpose home ranges throughout the year (Samuel et al. 1985, Stanton et al. 2014).

Social behaviors (e.g., territoriality) must be considered together with vegetation metrics for many species, particularly those with narrow niches and complex reproductive strategies. 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 space use (Newton 1994, Both and Visser 2003). 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 (Cockle et al. 2010, Farrell et al. 2012). For resident woodland birds like the cooperatively breeding Brown-headed Nuthatch (*Sitta pusilla*), 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).

The Red-cockaded Woodpecker is an ideal species for evaluating relative importance of social factors, conspecific density, and forest structure on space use. Red-cockaded Woodpeckers are reliant on mature, living pines (*Pinus* spp.) for excavating cavities and foraging (Jackson and Jackson 1986, Zwicker and Walters 1999). They are resident cooperative breeders that live in social groups consisting of the breeding pair and up to 5 helper individuals. Groups defend a territory that includes their cluster of cavity trees and adjacent foraging habitat (Ligon 1970, Hooper et al. 1982). Distribution of cavity trees drives Red-cockaded Woodpecker habitat use, dispersal, population density, and territorial behaviors (Walters 1990, Conner et al. 2001). Excavation of natural cavities can take years to complete, thus artificial cavities are essential tools for maintaining existing groups and establishment of new groups in unoccupied foraging habitat (Walters 1991).

Because foraging Red-cockaded Woodpeckers may avoid or be excluded from foraging habitat within the vicinity of neighboring group cavity tree clusters, understanding the scale-dependent effects of neighboring group density, territorial interactions, and distribution of cavity trees could aid managers in identifying the most appropriate spatial scale for Red-cockaded Woodpecker management. Based on results from other systems, the role of neighboring group density in Red-cockaded Woodpecker habitat use might be more important than previously recognized, especially for birds occupying artificial cavities in restored or intensively managed foraging habitat (e.g., Bennett et al. 2012, Stanton et al. 2015). For example, if foraging Red-cockaded Woodpeckers 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 Red-cockaded Woodpecker reproductive success or dispersal (Cox and Engstrom 2001, Pasinelli et al. 2004, Cox and McCormick 2016).

Our objective was to improve existing habitat models for the Red-cockaded Woodpecker by integrating fine-scale habitat structure with multi-scale covariates for population density, cavity tree locations, and territorial interactions. Specifically, we (1) conducted a scaling analysis to rank scale-dependent effects of territorial interactions, cavity tree locations, and conspecific density on space use by foraging Red-cockaded Woodpeckers; and (2) evaluated support among multi-scale models describing variation in Red-cockaded Woodpecker UDs in response to LiDAR-derived foraging habitat thresholds and scale-optimized covariates for territorial interactions, cavity tree locations, and conspecific density.

METHODS

Study Areas

The Savannah River Site, an 80,267 ha National Environmental Research Park owned and operated by the U.S. Department of Energy (DOE), is located on the Upper Coastal Plain and Sandhills physiographic provinces in South Carolina, USA (Figure 1). 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 DOE in 1951, the majority of the Savannah River Site was maintained in agricultural fields or had been harvested for timber (White 2005). The U.S. Department of Agriculture (USDA) 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 reforested with artificially regenerated stands of loblolly (*P. taeda*), longleaf (*P. palustris*), and slash (*P. elliottii*) pines, with an additional 2,832 ha of 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 the 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 DOE, the USDA Southern Research Station began management for the Red-cockaded Woodpecker in 1984 with the objective to restore a viable population on the Savannah River Site. Under intensive management since 1985, the Red-cockaded Woodpecker population has grown from 3 groups of 4 birds (Johnston 2005) to 91 groups of more than 250 birds (T. Mims personal communication). Management of Red-cockaded Woodpecker foraging habitat on the Savannah River Site has included implementing prescribed fire and other methods to control hardwood midstory, constructing recruitment clusters, and aggressively protecting existing cavity trees (Allen et al. 1993, Haig et al. 1993, Franzreb 1997). The Savannah River Site Red-cockaded Woodpecker population is designated as a secondary core population in the South Atlantic Coastal Plain recovery unit (USFWS 2003). All Red-cockaded Woodpeckers at the Savannah River Site are uniquely color-banded by USDA Forest Service personnel as part of ongoing monitoring.

The Carolina Sandhills National Wildlife Refuge, one of 14 Land Management and Research Demonstration areas managed by the U.S. Fish and Wildlife Service (USFWS), is located on the Atlantic Coastal Plain and Piedmont Plateau physiographic provinces, South Carolina, USA (Figure 1). The refuge is characterized by sandy soils dominated by upland, xeric pine woodlands. The refuge is $\sim$19,364 ha, including 14,164 ha of predominantly longleaf pine–turkey oak (*P. palustris*–*Q. cerris*) cover (USFWS 2010). The refuge harbors 150 active Red-cockaded Woodpecker clusters, representing the largest Red-cockaded Woodpecker population on USFWS lands. As part of ongoing monitoring efforts, refuge personnel monitor nests and band nestlings with aluminum bands and unique combinations of color bands.

Home-range Data

We collected home-range data for a sample of 44 Red-cockaded Woodpecker groups on the Savannah River Site ($n = 34$) and Carolina Sandhills National Wildlife Refuge ($n = 10$; Figure 1). We tracked individual Red-cockaded Woodpecker groups (hereafter, home-range follows) over a 4- to 8-hr period, recording location fixes at 15-min intervals (Franzreb 2006), twice a month between March 2013 and April 2015. Home-range follows consisted of sustained visual contact with individuals of the sample

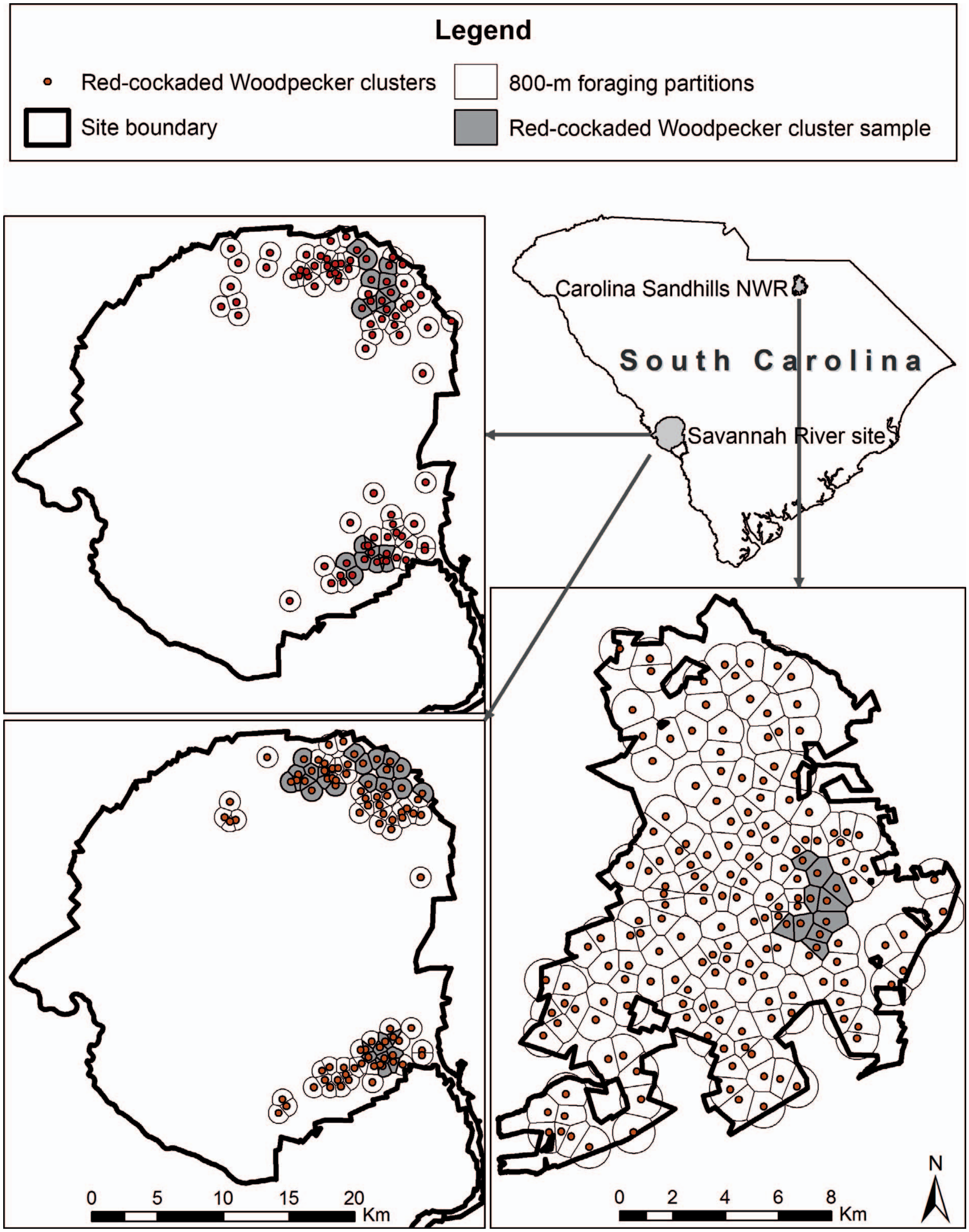

FIGURE 1. Spatial distribution and status of Red-cockaded Woodpecker cavity tree clusters on the Savannah River Site and Carolina Sandhills National Wildlife Refuge, South Carolina, in 2013 and 2014.

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). We recorded $\geq$15 location fixes throughout the day during each follow, thus providing $\geq$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. In addition to location fixes, we recorded basic behavior (foraging, resting, cavity work, feeding nestlings, or intraspecific interactions between neighboring groups) at each 15-min interval. Red-cockaded Woodpecker 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 used spotting scopes to resight unique color band combinations to ensure the breeding male was followed for each group. We also recorded the location of cavity tree starts (i.e. incomplete cavities in the process of excavation; USFWS 2003) observed during home-range follows.

LiDAR-derived Habitat Data

Following Garabedian et al. (2014a, 2017), we used high-resolution LiDAR-derived habitat thresholds to quantify the amount and condition of foraging habitat available to individual Red-cockaded Woodpecker groups on the Savannah River Site. 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 and processed using the FUSION program (McGaughey 2009, Reutebuch and McGaughey 2012). Garabedian et al. (2014a) used regression methods to relate the LiDAR sensor data to forest inventory measurements collected on 194 ground calibration plots distributed across a range of forest conditions on the Savannah River Site. They used the resulting regressions to predict forest structural attributes included in the Red-cockaded Woodpecker recovery plan (USFWS 2003) and subsequently populate raster layers at 20 m resolution across the entire Savannah River Site. An 80 m grain size was optimal for characterizing foraging habitat quality based on the objective to minimize prediction error while maintaining a grain size concordant with recommended methods for assessment and management of Red-cockaded Woodpecker foraging habitat (Garabedian et al. 2014a). Garabedian et al. (2017) used piecewise regression to characterize thresholds in use of 80 m LiDAR-derived habitat data by foraging Red-cockaded Woodpecker groups. Based on their results, we selected site-specific LiDAR-derived habitat thresholds for pines $\geq$35.6 cm dbh, pines $\geq$25.4 cm dbh, hardwoods $<$22.9 cm dbh, and hardwood canopy cover to represent potential foraging habitat on the Savannah River Site (Table 1). We maintained the 80 m grain size for each LiDAR-derived habitat variable and all subsequent layers. We used the Neighborhood and Extraction toolsets in the Spatial Analyst toolbox in ArcGIS to create spatially explicit datasets for use in subsequent models (ESRI 2014).

Data Analysis

Development of spatial and distance covariates. We developed spatial covariates for the number of neighboring Red-cockaded Woodpecker groups, the number of cavity tree starts, and the number of intraspecific interactions to characterize conspecific density, distribution of critical discrete resources, and territoriality for the sample of Red-cockaded Woodpecker groups ($n = 44$). We summarized the spatial covariates in a moving window analysis and assigned scale-specific discrete values to individual 80 m pixels within UDs of woodpecker groups for scaling analyses described below (Table 1). We recognize that using small buffers (i.e. 200 m) to summarize relatively large pixels (i.e. 80 m) may mask some fine-scale patterns of the spatial covariates. Additionally, we created a covariate for the Euclidean distance to groups' cavity tree clusters to account for central-place foraging behaviors (Rosenberg and McKelvey 1999).

Space-use estimation. We used fixed-kernel density methods and the reference bandwidth to estimate annual UDs for individual Red-cockaded Woodpecker groups on both sites ($n = 44$). Utilization distributions define space use as a continuous and probabilistic process and objectively delineate the extent of available habitat for each individual (Kertson and Marzluff 2011). We used 99% UD contours to delineate 80 m pixels (i.e. space) available to individual Red-cockaded Woodpecker groups and UD volume of each pixel to define the probability of use. We estimated separate UDs for each woodpecker group to correctly treat individual groups as the independent sampling unit and mitigate autocorrelation of relocations (Aebischer et al. 1993, Otis and White 1999). Additionally, use of smoothing functions offers the flexibility to specify a constant pixel size for each woodpecker UD without changing UD estimates or shape of the surface (Calenge 2011). Accordingly, we estimated UDs for individual Red-cockaded Woodpecker groups on the 80 m resolution spatial grid used for development of the LiDAR-derived habitat data and spatial covariates.

Model development and selection. We used resource utilization functions (RUFs; Marzluff et al. 2004) to model variation in Red-cockaded Woodpecker UD volume in response to LiDAR-derived habitat, distance, and spatial covariates. Resource utilization functions are multiple linear regressions fit on Matern correlation functions that account for autocorrelation among values of adjacent UD pixels that may bias coefficients (Hepinstall et al. 2003).

TABLE 1. Definitions of 80 m resolution covariates used to fit resource utilization functions for Red-cockaded Woodpecker groups on the Savannah River Site ($n = 34$) and Carolina Sandhills National Wildlife Refuge ($n = 10$), South Carolina. Data included LiDAR-derived estimates of forest structure and composition (LiDAR habitat thresholds), and multi-scale summaries of the number of neighboring groups (Knn), number of cavity tree starts (Starts), and the number of neighboring group interactions (Intrasp).

Variable type	Variable description
LiDAR habitat thresholds	
Pines ≥35.6 cm dbh	≥22 pines ha^{-1} that are ≥35.6 cm dbh
Pines ≥25.4 cm dbh	BA of pines ≥25.4 cm dbh is ≥2.3 m^2 ha^{-1}
Canopy hardwoods	Hardwood canopy cover ha^{-1} is <10%
Midstory hardwoods	BA of hardwoods 7.6-22.9 cm dbh is <0.4 m^2 ha^{-1}
Knn	
Knn200m	Number of Red-cockaded Woodpecker clusters within 200 m radii
Knn400m	Number of Red-cockaded Woodpecker clusters within 400 m radii
Knn800m	Number of Red-cockaded Woodpecker clusters within 800 m radii
Knn1600m	Number of Red-cockaded Woodpecker clusters within 1,600 m radii
Knn2000m	Number of Red-cockaded Woodpecker clusters within 2,000 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
Intraspecific	
Intrasp100m	Number of intraspecific interactions within 100 m radii
Intrasp200m	Number of intraspecific interactions within 200 m radii
Intrasp300m	Number of intraspecific interactions within 300 m radii
Intrasp400m	Number of intraspecific interactions within 400 m radii

Matern correlation functions are estimated in RUFs using maximum-likelihood techniques and require initial values for 2 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. Following Marzluff et al. (2004), we set initial values for the range of spatial dependence as the reference bandwidth for each woodpecker UD and the smoothness of each UD surface to 1.5. We fit RUFs using the R statistical environment (R Development Core Team 2015) and the contributed package ruf (Handcock 2015).

We adopted a two-stage approach for modeling Red-cockaded Woodpecker space use with RUFs in which we fit individual models for each woodpecker group and then averaged individual model coefficients for population-level inference (Marzluff et al. 2004). The average population-level coefficients were not confounded by autocorrelation because the individual RUFs themselves were independent and unbiased estimates (Fieberg et al. 2010). We fit RUFs for each woodpecker group using UD volume as the response and identical covariates, thus information-theoretic methods were suitable to rank competing models for individual woodpecker groups (Burnham and Anderson 2002). We used Akaike's Information Criteria (AIC; Akaike 1974) to rank models fit to data for individual Red-cockaded Woodpecker groups and used the most frequent top model(s) across individual groups to identify the most parsimonious model for the complete sample of woodpecker groups.

Scale optimization. Prior to fitting multi-scale RUFs, we conducted a univariate scaling analysis to identify the most parsimonious scale of response for spatial covariates among Red-cockaded Woodpecker groups on both sites ($n = 44$). We fit univariate RUFs to evaluate effects of the number of neighboring groups, cavity tree starts, and intraspecific interactions across multiple spatial extents while holding the pixel size constant at 80 m (Wheatley and Johnson 2009, McGarigal et al. 2016). We ranked univariate RUFs using AIC and retained each spatial covariate at the scale most frequently identified as the top model across individual woodpecker groups for use in pseudo-optimized multi-scale models (McGarigal et al. 2016).

Multi-scale models. We fit third-order (within home-range; Johnson 1980) multi-scale RUFs, each with the scale-optimized covariates for either the number of neighboring groups, intraspecific interactions, or cavity tree starts. In addition to the scale-optimized covariate in each model, we included distance to the cavity tree cluster and LiDAR-derived habitat thresholds as independent variables. In addition to accounting for central-place foraging behaviors, Euclidian distance to cavity tree clusters mitigated confounding effects from autocorrelation of habitat because high-quality habitat tends to be closer to cavity tree clusters (Rosenberg and McKelvey 1999, Betts et al. 2006). Because we did not have LiDAR-derived habitat data for the Carolina Sandhills National

TABLE 2. Spatial covariates resolved to 80 m grain sizes used to model variation in utilization distributions across multiple spatial extents (Extent) for Red-cockaded Woodpeckers groups on the Savannah River Site ($n = 34$) and Carolina Sandhills National Wildlife Refuge ($n = 10$), South Carolina, between April 2013 and March 2015. Values reported represent average number of neighboring groups (Knn), number of cavity tree starts (cavity starts), and the number of intraspecific interactions (intraspecific) within each Extent for groups on each study site.

		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	2.40	1.27	3.64	1.13
	1,600 m	7.02	2.42	12.90	2.52
	2,000 m	10.12	2.94	18.96	2.46
Cavity starts	200 m	0.47	0.52	0.41	0.49
	400 m	1.00	0.58	1.11	0.63
	600 m	2.66	1.17	3.65	2.51
	800 m	8.06	2.54	12.90	2.46
Intraspecific	100 m	1.16	2.24	1.85	2.46
	200 m	3.66	5.13	6.12	5.62
	300 m	7.33	8.63	12.14	8.77
	400 m	12.31	12.43	19.46	11.74

Wildlife Refuge, we only fit multi-scale RUFs for groups on the Savannah River Site in 2013 and 2014 ($n = 34$).

RESULTS

Home-range Data

The average duration of completed home-range follows was 5.5 hr (range 4–8 hr), resulting in over 36,000 Red-cockaded Woodpecker locations between April 2013 and March 2015. Approximately 34,000 locations were associated with foraging behaviors, with 648 locations during intraspecific interactions between neighboring groups. The remaining 1,500 locations represented ancillary behaviors such as resting, incubation, or cavity maintenance. We documented locations of 99 cavity tree starts.

Space-use Estimation

On average, we used 696 (SE = 57) foraging relocations to estimate Red-cockaded Woodpecker UDs. The reference bandwidths estimated for individual group UDs averaged 83 m (median 80 m; range 41.5–151.5 m). The total area of available habitat within boundaries of 99% UD volume contours averaged 135 ha and ranged from 48 to 304 ha.

Spatial Covariates

Spatial covariates exhibited similar trends across spatial extents on both study sites (Table 2). On average, the number of cavity tree starts was lowest within 200 m and progressively increased within each radius up to 800 m. The number of intraspecific interactions was lowest within 100 m and progressively increased within each radius up to 400 m (Table 2). The number of neighboring Red-cockaded Woodpecker groups was lowest within 200 m and progressively increased within each radius up to 2,000 m.

Scale Optimization

Comparison of univariate RUFs indicated spatial covariates summarized within 200 m and 400 m radii of pixels identified as part of the 99% UD for each group were the most parsimonious scales describing variation in Red-cockaded Woodpecker space use (Table 3). The number of neighboring groups and number of cavity tree starts were most parsimonious within 200 m of a UD pixel, with positive effects. The number of intraspecific interactions was most parsimonious within 400 m of a UD pixel, also with positive effects. We retained covariates for the number of neighboring groups and number of cavity tree starts within 200 m of a UD pixel, and the number of intraspecific interactions within 400 m of a UD pixel, for use in subsequent multi-scale RUFs.

Multi-scale Models

Model selection clearly indicated that the number and proximity to neighboring groups' cavity tree clusters were the most important predictors of Red-cockaded Woodpecker space use once baseline vegetation attributes existed in an area (Table 4). The most parsimonious multi-scale RUF for 22 of 34 groups included covariates for the number of neighboring groups within 200 m of a UD, LiDAR-derived habitat thresholds, and Euclidian distance to the cavity tree cluster. We detected negative effects of distance from the cavity tree cluster, and positive effects of the number of neighboring groups and each of the 4 LiDAR-derived habitat thresholds. The most parsimonious multi-scale RUF for 11 of 34 groups included the number

TABLE 3. Comparison of scale-specific effects of the number of neighboring Red-cockaded Woodpecker groups (Knn), number of intraspecific interactions (intraspecific), and number of cavity tree starts (cavity starts) on space use by woodpecker groups on the Savannah River Site ($n = 34$) and Carolina Sandhills National Wildlife Refuge ($n = 10$), South Carolina, between April 2013 and March 2015.

			Direction		
Parameter	Extent	Standardized $\bar{\beta}$ (SE)	+	−	Frequency top model
Knn	200 m	36.84 (0.07)	38	6	34
	400 m	20.77 (0.07)	31	13	6
	800 m	−0.65 (0.05)	28	16	2
	1,600 m	0.82 (0.04)	19	25	1
	2,000 m	2.47 (0.03)	17	27	1
Cavity starts	200 m	0.073 (0.0007)	30	14	26
	400 m	−0.076 (0.0003)	14	30	14
	600 m	−0.11 (0.0002)	18	26	3
	800 m	−0.11 (0.0002)	8	36	1
Intraspecific	100 m	1.70 (0.03)	26	18	4
	200 m	1.53 (0.02)	26	18	6
	300 m	1.42 (0.01)	39	5	6
	400 m	2.03 (0.01)	40	4	28

of cavity tree starts within 200 m of a UD pixel, LiDAR-derived habitat thresholds, and Euclidian distance to the cavity tree cluster. Multi-scale RUFs fit with LiDAR-derived habitat thresholds, and covariates for intraspecific interactions within 400 m of a UD pixel was the most parsimonious model for 1 of 34 groups.

DISCUSSION

Our results indicate fine-grained habitat use by foraging Red-cockaded Woodpeckers may be mediated by local population density such that Red-cockaded Woodpeckers may use the presence of neighboring groups as a

TABLE 4. Multi-scale resource utilization functions (RUF) fit to Red-cockaded Woodpecker group utilization distributions (UDs) on the Savannah River Site, South Carolina, 2014 ($n = 34$). Models were fit with Euclidian distance (m) to cavity tree clusters (cluster distance), LiDAR-derived habitat thresholds (LiDAR), plus covariates for either the number of neighboring groups (Knn) within 200 m of UD pixels, number of intraspecific interactions within 400 m of UD pixels (intraspecific), or number of cavity tree starts within 200 m of UD pixels (cavity starts).

RUF Model	Unstandardized $\bar{\beta}$ (SE)	Standardized $\bar{\beta}$ (SE)	Frequency top model
Knn + LiDAR[a]			22
Cluster distance	−0.10 (0.0004)	−0.61 (1.1E−11)	
Knn	11.74 (0.11)	0.35 (9.7E−5)	
DLP22	2.88 (0.24)	0.002 (3.4E−4)	
BAMP2.3	2.65 (0.11)	0.03 (2.2E−5)	
BASH0.4	4.36 (0.10)	0.15 (1.2E−5)	
HWCC10	8.16 (0.11)	0.03 (6.4E−5)	
Cavity starts + LiDAR			11
Cluster distance	−0.11 (0.0005)	−0.71 (2.4E−11)	
Cavity starts	−0.02 (0.0005)	−0.13 (1.1E−14)	
DLP22	1.47 (0.24)	−0.02 (1.6E−4)	
BAMP2.3	2.14 (0.11)	0.06 (1.8E−5)	
BASH0.4	6.33 (0.10)	0.16 (3.5E−5)	
HWCC10	6.87 (0.12)	0.07 (5.6E−5)	
Intraspecific + LiDAR			1
Cluster distance	−0.13 (0.0004)	−0.81 (1.1E−11)	
Intraspecific	−0.009 (0.0004)	−0.05 (2.5E−12)	
DLP22	2.41 (0.24)	−0.01 (3.1E−12)	
BAMP2.3	2.35 (0.11)	0.07 (2.6E−5)	
BASH0.4	6.32 (0.10)	0.16 (3.2E−5)	
HWCC10	8.41 (0.12)	0.05 (6.5E−5)	

[a] DLP22 = foraging habitat with ≥22 pines ≥35.6 cm dbh ha^{-1}; BAMP2.3 = foraging habitat with ≥2.3 m^2 ha^{-1} basal area (BA) of pines ≥25.4 cm dbh; BASH0.4 = <0.4 m^2 ha^{-1} BA of hardwoods 7.6–22.9 cm dbh; HWCC10 = foraging habitat with <10% hardwood canopy cover ha^{-1}.

proximate indicator of habitat quality. Once baseline vegetation thresholds were satisfied, the distribution of neighboring groups within 200 m of Red-cockaded Woodpecker home ranges was the predominant variable predicting space use by foraging Red-cockaded Woodpeckers.

Foraging Red-cockaded Woodpeckers 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 Red-cockaded Woodpeckers in high-quality foraging habitat detected in our study. Prolonged episodes of arthropod exhaustion on pines selected by foraging Red-cockaded Woodpeckers are likely rare due to movement of arthropods up the pine bole from the understory (Hanula and Franzreb 1998), so it is unlikely Red-cockaded Woodpeckers would use neighboring groups as a cue for abundant arthropod prey items. Previous research demonstrated Red-cockaded Woodpeckers forage on a variety of arthropods, but select similar arthropod prey to provision nestlings on sites representing high- and low-quality habitat (Hanula and Engstrom 2000, Hanula et al. 2000). Because abundance of arthropod prey available to foraging Red-cockaded Woodpeckers 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 Red-cockaded Woodpeckers may aggregate in areas with more neighboring groups to gain cues on neighbors during prospecting behaviors prior to juvenile dispersal (Pasinelli and Walters 2002). Natal dispersal decisions are contingent on social and environmental conditions on and around the natal territory (Kesler and Walters 2012), which could be why we detected strong positive responses to neighboring groups and foraging habitat structure by foraging Red-cockaded Woodpeckers. Given proximity to multiple groups is important to dispersal success of both juvenile and breeding females (Daniels and Walters 2000), it is likely that dense aggregations of neighboring groups are advantageous for dispersing Red-cockaded Woodpeckers by indirectly 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 indicates the distribution and density of neighboring Red-cockaded Woodpecker groups has a greater impact on habitat use and movements by Red-cockaded Woodpeckers than does foraging habitat structure.

Assuming a template of homogeneous high-quality habitat, if dispersing Red-cockaded Woodpeckers are unable to find suitable destination groups, which often occurs in isolated groups (USFWS 2003), the benefits dispersing individuals confer on group persistence through breeder replacement may be minimized, thus reducing the number of potential breeding groups. Because larger Red-cockaded Woodpecker groups are correlated with increased reproductive success and breeder survival (Khan and Walters 2002), and ~50% of male fledglings and most female fledglings disperse or die (Walters et al. 1988b), isolation from neighboring groups could indirectly limit breeder replacement and consequently group persistence (Schiegg et al. 2002). Additionally, the number and proximity to neighboring groups could be particularly beneficial for juvenile females that disperse to avoid inbreeding and for breeding females that disperse to new groups between seasons (Daniels and Walters 2000). Such benefits may offset reduced fitness driven by increases in competitive interactions (Zack 1990, Garabedian 2017) and potential inbreeding depression (Schiegg et al. 2006) for neighboring groups under high density conditions.

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

High spatial resolution of Red-cockaded Woodpecker UDs allowed us to map potential Red-cockaded Woodpecker habitat as a continuum of quality that improved precision of potential habitat maps in comparison to current approaches (e.g., the Red-cockaded Woodpecker 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 Red-cockaded Woodpeckers to hardwood midstory encroachment at fine grains (80 m grains; Garabedian et al. 2017), the current Red-cockaded Woodpecker Matrix Habitat Model does not incorporate fine-grained habitat structure or habitat use needed to detect these responses within stands. Varying grain sizes of individual LiDAR-derived habitat attributes may offer further improvements to model fit, offer insight into the scale at which Red-cockaded Woodpeckers respond consistently to specific pine size classes in the species' foraging habitat guidelines, and improve precision of habitat maps (Gottschalk et al. 2011). Because selection of pines by foraging Red-cockaded Woodpeckers shifts with availability across the species' range (Zwicker and Walters 1999), a multi-grained approach could allow managers to target specific pine size classes based on local forest structure. For example, on second-growth forests with few isolated relic old-growth pines or otherwise limited distribution of pines $\geq$35.6 cm dbh across the landscape (e.g., Fort Bragg and Savannah River Site in early 1990s; Walters et al. 2002b, Franzreb 2006), 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 $\geq$25.4 cm dbh used primarily for foraging. Such information can help managers use limited resources to their fullest potential in Red-cockaded Woodpecker habitat conservation as populations continue to grow and require additional foraging and nesting habitat (Reed et al. 1988).

Spatial criteria are especially important in development of guidelines for strategic management of neighboring Red-cockaded Woodpecker 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 Red-cockaded Woodpecker habitat remains unoccupied. Current recovery guidelines were developed using data from relatively low-density conditions, and could be modified to provide better management guidelines in restored habitat with extremely high population densities (Azevedo et al. 2000). For example, group density targets provided in the current recovery guidelines ($\sim$1 group 150–250 ha^{-1}; USFWS 2003) are nearly 4 times lower than densities observed for productive groups ($\sim$1 group 45 ha^{-1}; Engstrom and Sanders 1997). Development of spatial criteria to guide management of dense aggregations of recruitment clusters in restored habitat could provide managers the flexibility to balance such increases in group density with other management objectives (e.g., strategic placement of recruitment clusters, timber harvest). Dense aggregations of recruitment clusters strategically placed in unoccupied habitat may act as stepping-stones that connect spatially distinct Red-cockaded Woodpecker subpopulations on the Savannah River Site (Saenz et al. 2002, Trainor et al. 2013). Populations as small as 25 potential breeding groups can persist for decades if highly aggregated in space (Walters et al. 2002a). High densities of Red-cockaded Woodpecker recruitment clusters ($\sim$1 cluster 25 ha^{-1}) may also improve success of translocation events by increasing the likelihood that multiple potential breeding groups will become established in unoccupied habitat (Carrie et al. 1999, Cox and Engstrom 2001). These high densities, however, do increase the likelihood of captured clusters where one Red-cockaded Woodpecker group occupies a neighboring cluster in addition to their breeding cluster (USFWS 2003).

Spatially explicit habitat models that include covariates for the local social environment offer improved predictive power and thus more useful tools to guide conservation of endangered species with complex social systems (Ahlering and Faaborg 2006, Campomizzi et al. 2008). Several birds of conservation concern use social cues from conspecifics in habitat selection (Fletcher 2007, Nocera and Betts 2010) that in turn have been shown to influence reproduction (Brown et al. 2000, Pärt et al. 2011), survival (Brown et al. 2016), and dispersal (Serrano and Tella 2003). Our study highlights the importance of social factors in predicting Red-cockaded Woodpecker habitat use, potentially due to increased demographic connectivity and associated benefits to dispersal and breeder replacement in dense aggregations of Red-cockaded Woodpecker groups (Azevedo et al. 2000, Herbez et al. 2011, Zeigler and Walters 2014). Red-cockaded Woodpeckers are affected strongly by isolation due to limited dispersal abilities, a problem also faced by other cooperatively breeding species (Walters et al. 1988a, Koenig et al. 1992, Sharp et al. 2008). Demographic isolation and disrupted social environments in fragmented habitat have been linked to the decline of several treecreepers (*Climacteris rufa*, *C. picumnus*, *C. affinis*; Walters et al. 1999, Luck 2000, Cooper and Walters 2002, Radford and Bennett 2004). By considering both habitat and social factors, there is greater potential to develop targeted conservation strategies that mitigate effects of isolation on social bird populations in restored habitat. Specifically, the scale at which species' response to conspecifics is strongest may be the scale at which reintroduction and colonization of restored habitat is most effective (Andrews et al. 2015, Hunt et al. 2017), and that scale may be surprisingly small (e.g., this study, Albrecht-Mallinger and Bulluck 2016).

ACKNOWLEDGMENTS

We 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. We thank A. Poole with the USDA Forest Service-Savannah River for assistance in developing LiDAR raster layers. M. Pavlosky, Jr., A. Sager, D. Hunter, C. Hansen, and J. Spickler assisted with field data collection. Additionally, T. Grazia, N. Jordan, T. Mims, and J. Nance provided historic Red-cockaded Woodpecker data and facilitated site access throughout the study.

We thank J. Blake, T. R. Simons, and 3 anonymous reviewers for valuable discussions and comments that improved the quality of the manuscript.

Funding statement: Funding was provided by 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.

Ethics statement: We adhered to the ethics protocols of the USDA Forest Service, US Fish and Wildlife Service, and North Carolina State University.

Author contributions: J.E.G., C.E.M., M.N.P., and J.C.K. conceived the idea, design, and experiment (supervised research, formulated question or hypothesis). J.E.G. performed the experiments (collected data, conducted the research). J.E.G., C.E.M., M.N.P., and J.C.K. wrote the paper. J.E.G. developed or designed the methods and analyzed the data.

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