RESEARCH ARTICLE

Scale-dependent and multi-metric nest habitat thresholds for Red-headed Woodpeckers at the northern periphery of their range

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ABSTRACT

The relation between species occurrence and the structure or composition of habitat can be complex and often varies in a species-specific manner. Sometimes, species–habitat relations are defined by thresholds, or abrupt nonlinear responses to a habitat gradient. Threshold responses are expected when certain habitat features are required for species occurrence. For example, primary cavity-nesting woodpeckers often typify the threshold concept because in the absence of appropriate substrates (decadent wood) large enough for nest cavities, woodpeckers will not occur. In such cases, identifying thresholds is important to ensure that management activities meet minimal (or maximal) habitat requirements of target species. The Red-headed Woodpecker (*Melanerpes erythrocephalus*) is a species of national conservation concern, and loss of suitable nesting habitat has been suggested as a primary factor in its population declines. Threshold responses may partly explain why this species has gone locally extinct in areas where land-use change resulted in a transition from suitable to unsuitable habitat. Here, we tested whether a regionally important population of Red-headed Woodpeckers in northern New York, near the periphery of the species' range, exhibited threshold responses in their selection of nesting habitat. We used boosted regression trees (BRT) to identify nest habitat thresholds in relation to multiple habitat variables at multiple spatial scales (nest tree, forest patch, and forest stand). We identified nest tree thresholds related to tree decay class ($\geq$33% decadent canopy), cumulative dead limb length ($\geq$4 m), and tree diameter ($\geq$34 cm dbh). Forest patch (vegetation surrounding nest tree; 0.04 ha) thresholds were related to cumulative dead limb length ($\geq$17 m), woody understory height (<12 cm), mean tree diameter (30 cm dbh), and large tree ($\geq$30 cm dbh) density of $\geq$4. Forest stand thresholds were related to overall stand decadence (on average trees have $\geq$1% crown decay) and woody understory height (<12 cm). Red-headed Woodpeckers exhibited scale-dependent and multi-metric nest habitat thresholds, which indicate that a lack of suitable nesting habitat (i.e. habitats meeting or exceeding multi-metric and multi-scale criteria) may be limiting population growth near the periphery of the species' range. In particular, the abundance of decadent (dead and decaying) tree resources appears to limit the distribution of suitable habitat. Our objective threshold criteria can be used to identify habitats of high conservation value for this species, or to identify specific habitat features that require management or restoration to increase suitable habitat for this threatened species.

Keywords: habitat thresholds, *Melanerpes erythrocephalus*, nest habitat selection, New York, oak woodlands, Red-headed Woodpecker

Determinación de umbrales dependientes de la escala y del hábitat del nido para *Melanerpes erythrocephalus* en el borde norte de su distribución

RESUMEN

La relación entre la presencia de especies y la estructura o la composición del hábitat puede ser compleja y usualmente varía de una manera específica para cada especie. Muchas veces, las relaciones entre las especies y el hábitat son definidas por umbrales, o respuestas abruptas no lineales a un gradiente del hábitat. Se esperan encontrar respuestas a los umbrales cuando se requieren ciertas características del hábitat para la presencia de una especie. Por ejemplo, los carpinteros que anidan en cavidades que ellos mismos excavan usualmente tipifican el concepto de umbral, porque en ausencia de sustratos apropiados (madera en descomposición) lo suficientemente grandes para albergar las cavidades de sus nidos, los carpinteros no se encuentran presentes. En estos casos, es importante identificar los umbrales que aseguren que las actividades de manejo procuren los requerimientos mínimos (o máximos) de hábitat para las especies seleccionadas. *Melanerpes erythrocephalus* es una especie de interés nacional de conservación, y se ha sugerido que la pérdida de hábitat adecuado para anidar es un factor importante que determina las disminuciones poblacionales. Las respuestas a los umbrales pueden explicar parcialmente por qué esta especie se ha extinto localmente en áreas donde

el cambio de uso del suelo generó una transición de hábitat apropiado a hábitat inadecuado. Aquí, evaluamos si una población regionalmente importante de *M. erythrocephalus* en el norte de Nueva York, cerca del borde de distribución de la especie, mostró respuestas a los umbrales en su selección del hábitat de anidación. Usamos árboles de regresión potenciados para identificar los umbrales del hábitat de anidación considerando múltiples variables del hábitat a múltiples escalas espaciales (árbol del nido, parche de bosque y rodal de bosque). Identificamos los umbrales del árbol del nido relacionados con la clase de descomposición del árbol ($\geq$33% dosel decadente), el largo acumulativo del tronco muerto ($\geq$4 m) y el diámetro ($\geq$34 cm dap). Los umbrales del parche de bosque (la vegetación que rodea al árbol del nido; 0.04 ha) estuvieron relacionados con el largo acumulativo del tronco muerto ($\geq$17 m), la altura del sotobosque leñoso (<12 cm), el diámetro medio del árbol (30 cm dap) y el largo del árbol ($\geq$30 cm dap) de densidad $\geq$4. Los umbrales del rodal de bosque estuvieron relacionados con el deterioro general del rodal (los árboles promedio tienen $\geq$1% de deterioro de la copa) y con la altura media del sotobosque leñoso (<12 cm). *M. erythrocephalus* mostró umbrales dependientes de la escala y del hábitat del nido considerando múltiples métricas, que indican que la falta de hábitat adecuado de anidación (i.e. los hábitats que alcanzan o exceden los criterios de métricas y escalas múltiples) puede estar limitando el crecimiento poblacional cerca del borde de distribución de la especie. En particular, la abundancia de los recursos arbóreos en descomposición (muertos o deteriorados) parece limitar la distribución del hábitat adecuado. Nuestro criterio de umbral objetivo puede ser usado para identificar hábitats de alto valor de conservación para esta especie, o para identificar rasgos específicos del hábitat que requieren ser manejados o restaurados para aumentar los hábitats adecuados para esta especie amenazada.

Palabras clave: bosques de roble, *Melanerpes erythrocelphalus*, Nueva York, selección del hábitat de anidación, umbrales de hábitat

INTRODUCTION

Knowing species–habitat relations is a prerequisite for effective management of imperiled populations. However, the relation between species occurrence and the structure or composition of habitat varies in a species-specific manner and includes both linear and nonlinear responses. For example, some species exhibit threshold responses to the amount, distribution, or structure of habitat (Lindenmayer and Luck 2005). When habitat thresholds exist, the probability of species occurrence is defined by a unidirectional and abrupt nonlinear response curve along a habitat gradient (Ficetola and Denoel 2009), and habitat patches must meet or exceed threshold values for a species to occur. In such cases, identification of thresholds in species–habitat relations can be a useful tool to establish objective habitat management guidelines that meet the minimum (or maximum) requirements for target species (Huggett 2005, Muller and Butler 2010).

Primary cavity-nesting birds typify the threshold concept in their selection of nesting habitat because certain habitat characteristics (e.g., cavity substrates) are often required for suitable nesting conditions (Angelstam et al. 2003). Additionally, intense inter- and intra-specific competition for nest sites within the cavity-nesting community may constrain nest habitat for some individuals (Martin et al. 2004). Indeed, nest habitat thresholds have been documented for several woodpecker species— often related to the presence of decadent (dead and decaying) wood (e.g., Butler et al. 2004, Muller and Butler 2010, Touihri et al. 2014). Consequently, cavity-nesting species can be sensitive to human-mediated changes to habitat structure or composition, because minor changes in habitat conditions can result in rapid transition from suitable to unsuitable habitat when threshold criteria are not met. This is particularly relevant for species of conservation concern, where maintaining suitable habitat is a conservation priority.

The Red-headed Woodpecker (*Melanerpes erythrocephalus*) is a primary cavity-nesting species that is broadly distributed throughout the eastern United States, yet populations have steadily declined in recent decades (Sauer et al. 2014). Consequently, Red-headed Woodpeckers are listed as threatened in several states and are considered a species of national conservation concern (Rich et al. 2004). Throughout its range, the Red-headed Woodpecker's nesting habitat consists of a variety of disparate habitat types, such as oak (*Quercus* spp.) and pine (*Pinus* spp.) savanna, river bottom forest, burned ponderosa pine (*P. ponderosa*) forest, cottonwood and aspen (*Populus* spp.) riparian woodlands, agricultural woodlots, campgrounds, suburban parks, and golf courses (Conner 1976, Sedgwick and Knopf 1990, Vierling and Lentile 2006, Atterberry-Jones and Peer 2010, Kilgo and Vukovich 2012, Hudson and Bollinger 2013). In much of the range the species is partially or completely migratory, although its seasonal movements are poorly described (Smith et al. 2000, Vukovich and Kilgo 2013). Although these habitat types differ in vegetation community composition, they retain similar structural properties that Red-headed Woodpeckers require. In particular, the importance of large decadent trees and snags for use as nest trees, with surrounding vegetation characterized by open understories, low basal area of trees, and high densities of dead limbs, is well known (Sedgwick and Knopf 1990, Rodewald et al. 2005, King et al. 2007, Frei et al. 2013). Habitats that characterize these structural attributes have diminished in recent decades due to

land-use change, and a reduction in suitable breeding habitat is suggested as an important factor limiting Red-headed Woodpecker populations (Smith et al. 2000, Kilgo and Vukovich 2014). Therefore, increasing the distribution and quality of nesting habitat will be important for the recovery of this species (Smith et al. 2000).

Red-headed Woodpeckers are known to exhibit threshold responses to nesting habitat, and King et al. (2007) previously identified a nest habitat threshold for Red-headed Woodpeckers in central Wisconsin, near the core of their range, related to the density of dead limb–bearing trees surrounding the nest site. However, species–habitat relations can vary across a species' range (e.g., Zhu et al. 2012), and nest habitat thresholds for Red-headed Woodpeckers may correspondingly vary throughout their broad range. Red-headed Woodpecker population decline has been particularly severe near the periphery of the species' range in the northeastern United States (McGowan and Corwin 2008, Sauer et al. 2014), and these peripheral populations may experience resource limitations that shape their species–habitat relations (Brown 1984). Substantial population decline often results in species range contraction (Rodriguez 2002), and as such peripheral populations are important for maintaining long-term population persistence and genetic diversity—particularly when confronted with potential large-scale changes in land use (Lesica and Allendorf 1995). Given the broad distribution and wide variety of habitat types used by Red-headed Woodpeckers, it is important to obtain regionally specific and scale-dependent estimates of resource use on which to base management decisions. As such, testing for nest habitat thresholds in other regions, habitat types, and spatial scales can validate the usefulness of the threshold concept as it is applied to the conservation and management of this threatened species.

Here, we investigate Red-headed Woodpecker nest habitat selection in northern New York, at the extreme northeastern periphery of the species' range. Our objectives were twofold. First, we determined the relative influence of structural habitat characteristics (e.g., vegetation densities and decadent wood resources) on nest habitat selection at three spatial scales (nest tree, forest patch, and forest stand). We then sought to identify scale-dependent and multi-metric nest habitat thresholds by examining plots of these species–habitat relations for abrupt changes in slope along a habitat gradient.

STUDY AREA

We worked on Fort Drum (44°00′ N, 75°49′ W), a large (43,442 ha) active United States Army installation in northern New York (Figure 1). Much of the installation (approximately 70%, ~30,000 ha) is forested, consisting of mixed northern hardwoods dominated by sugar maple

(*Acer saccharum*), American beech (*Fagus grandifolia*), white ash (*Fraxinus americana*), and eastern white pine (*P. strobus*), and early successional habitat with associations of red maple (*A. rubrum*), gray birch (*Betula populifolia*), and quaking aspen (*P. tremuloides*) (Dobony et al. 2011). Our study area was located on a small portion of the installation characterized by sandy soils and open grasslands interspersed by forest stands consisting mostly of oak-dominated woodlands (this habitat type represents ~3%, ~1,500 ha, of the installation). We partitioned the study area into 35 forest stands ($\bar{x} = 9.0$ ha $\pm$ 1.0 SE) that were delineated from Fort Drum's forest inventory data (Fort Drum Forest Management Program, 2012). We selected these forest stands for study a priori based on historic use by Red-headed Woodpeckers on the installation (J. Bolsinger, personal observation). Forest stands varied in tree composition and structure, but were generally dominated by northern red oak (*Q. rubra*) and eastern white oak (*Q. alba*); other common trees included red maple, red pine (*P. resinosa*), eastern white pine, gray birch, and bigtooth aspen (*P. grandidentata*). Understory vegetation was characterized by woody shrubs including lowbush blueberry (*Vaccinium angustifolium*), Labrador tea (*Rhododendron groenlandicum*), and seedlings from overstory trees, while herbaceous vegetation was dominated by grasses (Poaceae), sedges (Cyperaceae), and ferns (Polypodiales).

METHODS

Nest Searching and Monitoring

We conducted nest searching from early May to late June during two breeding seasons (2012 and 2013). We systematically surveyed forest stands in linear transects and used audio playbacks of Red-headed Woodpecker calls and drumming at 200-m intervals to elicit responses from territorial pairs (protocol following Dudley and Saab 2003). Breeding Red-headed Woodpeckers are highly territorial and generally respond well to playback calls (Rodewald et al. 2005; J. Berl, personal observation). All forest stands were surveyed 3 times per season, and we separated individual surveys by at least one week. When adult Red-headed Woodpeckers were detected along survey transects we used behavioral cues (e.g., nest excavation, copulation, and chatter calls) to locate nest cavities. If we detected an individual on a survey but did not locate a nest cavity during the initial contact and observation, we returned to the site on ≥ 2 additional occasions to determine if the area contained a breeding territory.

Once potential nests were identified, we confirmed nesting activity by inspecting cavity contents using a wireless video camera (Luneau and Noel 2010) affixed to a telescoping fiberglass pole. In instances when we were unable to view cavity contents due to nest height (i.e. >14

FIGURE 1. Location of the study area and forest stands on Fort Drum Military Installation, New York.

m) or vegetative obstruction, we confirmed nesting activity if we (1) observed adults enter the nest cavity and remain for ≥5 minutes, (2) observed adults provisioning young, or (3) heard nestling vocalizations.

Habitat and Vegetation Measurements

We recorded extensive habitat data at 4 spatial scales by measuring characteristics of the (1) nest cavity, (2) nest tree, (3) forest patch (i.e. vegetation surrounding the nest tree), and (4) forest stand used by Red-headed Woodpeckers (encompassing second-, third-, and fourth-order selection sensu Johnson 1980). We constrained our vegetation sampling from July 1 to July 31 of each year to control for seasonal changes in vegetation structure and composition. All vegetation measurements were conducted by the same individual (J. Berl) to maintain consistency.

Nest cavity, nest tree, and forest patch characteristics. At the nest cavity, nest tree, and forest patch spatial scales, we collected habitat variables following Sedgwick and Knopf (1990) with minor modifications (see Table 1 for description of habitat variables). We directly measured characteristics of nest cavities and nest trees, while forest patch characteristics were recorded within 0.04-ha (11.3-m radius) circular plots centered on the nest tree (Martin et al. 1997). To evaluate nest tree and forest patch selection in relation to available habitat, we collected habitat data at random availability plots ($n = 50$) dispersed among forest stands that were occupied ($n = 11$) by a territorial Red-headed Woodpecker pair in at least one year of the study. We ensured that the number of availability plots per occupied forest stand ($\bar{x} = 2.0 \pm 0.26$ SE) was proportional to stand area, and confirmed that all availability plots were ≥ 25 m from known nest trees. Availability plots were located using a random point generator. We centered availability plots on a focal tree (≥ 10 cm dbh) located nearest the randomly selected coordinates and conducted vegetation measurements identical to those at nest sites (Table 1) with the exception of nest cavity characteristics.

Forest stand characteristics. We evaluated forest stand selection by comparing vegetative characteristics between forest stands that were occupied ($n = 11$) and unoccupied ($n = 24$) by Red-headed Woodpeckers. Forest stands were classified as occupied if they were used (i.e. we identified a nest tree and breeding territory within forest stand boundaries) by a territorial pair in at least one year of the study. We measured forest stand characteristics by randomly distributing stand inventory plots (0.04-ha circular plots; $n = 155$) throughout forest stands using a random point generator. The total number of inventory plots distributed per forest stand ($\bar{x} = 4.42 \pm 0.50$ SE, range $= 2$–16) was proportional to forest stand size, and we ensured that at minimum 1% of the total stand area was sampled in each year. We summarized forest stand variables (Table 1) for use in analyses by averaging values among individual plots within each stand.

Analytical Methods

Nest cavity characteristics. We were unable to compare characteristics of nest cavities to available cavities because too few ($n = 5$) random focal trees contained cavities. We report descriptive data on characteristics of occupied cavities including their height (m), orientation, and location on the tree (Table 1).

Nest habitat thresholds. We used boosted regression trees (BRT) to model differences in habitat characteristics between used and available habitat at each spatial scale (nest tree, forest patch, and forest stand). BRTs construct a large number of simple regression trees that recursively partition the response variable given a candidate set of predictor variables, and then use a stochastic machine learning technique (boosting) to ensemble individual regression trees—a procedure that greatly improves model predictive performance (De'ath and Fabricius 2000, Elith et al. 2008). We selected this analysis over traditional generalized linear model approaches (i.e. logistic regression) because BRTs are able to model complex nonlinear relations (Elith et al. 2008) that are required to identify thresholds in species–habitat relations (Ficetola and Denoel 2009). Furthermore, BRTs are robust to multi-collinearity among predictor variables and can accommodate data from virtually any distribution (Elith et al. 2008). This enabled us to incorporate all collected predictor variables into BRT models without the need for data transformation or culling of variables due to multi-collinearity.

We constructed BRT models using the "dismo" package (Hijmans et al. 2013) in program R version 2.13.1 (R Core Development Team 2011) and specified a Bernoulli response distribution to accommodate our binary (used versus available) data structure (Elith et al. 2008). Fitting BRT models requires the specification of several model parameters, including the model learning rate (specifies the contribution of each simple regression tree to the boosted model), the bag fraction (determines the proportion of model training data used), and tree complexity (determines the number of modeled interactions). Model parameters were set as following Elith et al. (2008) and varied to maximize model fit, with learning rate $= 0.005$, tree complexity $= 1$, and bag fraction $= 0.50$–0.90. Although BRTs are capable of modelling multi-way interactive effects among predictor variables (i.e. tree complexity >1), we chose to exclude interactions within our models because we were only interested in evaluating the direct relations between individual predictor variables and nest habitat selection to identify thresholds. Furthermore, preliminary analyses revealed that modeling interactions jeopardized model fit, and we therefore chose the more parsimonious procedure. We used 10-fold cross-validation to calculate the optimal number of regression trees for each BRT model using the "gbm.step" function (Hijmans et al. 2013). Model predictive performance was assessed using cross-validated estimates of area under the curve (AUC) of the receiving operator characteristic (ROC), which is a measure of model discrimination efficiency. We considered models with AUC scores ≥ 0.70 to have acceptable discrimination efficiency and models with AUC scores ≥ 0.90 to have excellent discrimination efficiency.

The relative influence of each predictor on the response was assessed by the average number of times a given predictor variable was selected for partitioning and weighted by the squared model improvement resulting from the successive partitions (Elith et al. 2008). We then used a cross-validated simplification algorithm to sequen-

TABLE 1. Habitat variables collected at multiple spatial scales to evaluate Red-headed Woodpecker habitat selection on Fort Drum Military Installation, New York, during May–August, 2012–2013.

Habitat variable	Description
Nest cavity	
Cavity height (m)	Estimated using a clinometer
Cavity diameter (cm)	Measured with ruler affixed to a telescoping pole
Cavity location	Bole or limb of tree
Substrate diameter (cm)	Diameter of substrate at cavity location; measured with ruler affixed to a telescoping pole
Cavity age	New or old cavity
Cavity orientation	Recorded with compass while directly facing cavity and taking back-azimuth
Substrate condition	Condition of the substrate surrounding the nest cavity; dead or alive
Tree[a]	
Tree species	Recorded when determinable
Tree dbh (cm)	Measured using calipers
Tree height (m)	Estimated using a clinometer
Limb tree	Presence/absence of dead limb, $\geq$10 cm diameter and with no vegetation growth
No. of dead limbs	Number of dead limbs, $\geq$10 cm diameter and with no vegetation growth
Cumulative dead limb length (m)	Summed length of dead limbs on focal tree; limbs $\geq$10 cm diameter and with no vegetation growth
Tree decay class	Tree decay class, ranked 1–8, following Newell et al. (2009): 1 = vigorous tree, 2 = <33% dieback, 3 = 33–66% dieback, 4 = >66% dieback, 5 = recently dead tree, 6 = dead tree, only large limbs remain, 7 = dead tree, only bole >6 m remains, 8 = dead tree, only bole <6 m remains
Tree state	Live or dead
Tree top condition	Unbroken or broken
Tree bark	Visually estimated % bark coverage and assigned to 4 coverage categories (0–25, 26–50, 51–75, 76–100)
Forest patch[b]	
Mean tree dbh (cm)	Mean dbh of trees $\geq$5 cm dbh
Canopy height (m)	Calculated as the mean height of 5 largest trees nearest the nest tree
Canopy cover (%)	Mean of 4 densiometer readings recorded at the plot edges in the 4 cardinal directions
Understory height (cm)	Mean height of woody understory vegetation (<0.5 m) recorded along 5 m transect from focal tree
Dead limb density	Mean number of dead limbs per tree, $\geq$10 cm diameter and with no vegetation growth
Cumulative dead limb length (m)	Summed length of dead limbs on trees within plot; limbs $\geq$10 cm diameter and with no vegetation growth
Mean tree decay class	Mean decay class for trees $\geq$5 cm dbh. Ranked 1–8, defined following Newell et al. (2009)
Snag density	Density of snags; $\geq$10 cm dbh
Dead limb tree density	Density of trees with $\geq$1 decadent limb, $\geq$10 cm diameter and with no vegetation growth
Small tree density	Density of small trees; 5–15 cm dbh
Medium tree density	Density of medium trees; 15–30 cm dbh
Large tree density	Density of large trees; >30 cm dbh
Total tree density	Density of all trees; $\geq$5 cm dbh
Forest stand[c]	
Stand area (ha)	Area of forest stand
Mean tree dbh (cm)	Mean dbh of trees $\geq$5 cm dbh
Canopy height (m)	Mean height of 5 largest trees nearest the nest tree
Canopy cover (%)	Mean of 4 densiometer readings recorded at the plot edges in the 4 cardinal directions
Understory height (cm)	Mean height of woody understory vegetation (<0.5 m) recorded along 5 m transect from focal tree
Dead limb density	Mean number of dead limbs per tree, $\geq$10 cm diameter and with no vegetation growth
Cumulative dead limb length (m)	Summed length of dead limbs on trees within plot; limbs $\geq$10 cm diameter and with no vegetation growth
Mean tree decay class	Mean decay class for trees $\geq$5 cm dbh. Ranked 1–8, defined following Newell et al. (2009)
Snag density	Density of snags; $\geq$10 cm dbh
Dead limb tree density	Density of trees with $\geq$1 decadent limb; $\geq$10 cm diameter and with no vegetation growth

TABLE 1. Continued.

Habitat variable	Description
Shrub density	Density of woody stems; 0.5–1.5 m in height
Sapling density	Density of saplings; 0–5 cm dbh
Small tree density	Density of small trees; 5–15 cm dbh
Medium tree density	Density of medium trees; 15–30 cm dbh
Large tree density	Density of large trees; >30 cm dbh
Total tree density	Density of all trees; ≥5 cm dbh

[a] Measured at the nest tree and random focal tree
[b] Measured within 0.04-ha plots centered on nest tree and random focal tree
[c] Measured within 0.04-ha stand inventory plots and summarized (averaged) for each stand

tially remove predictor variables that contributed little to model performance, as measured by changes in predictive deviance (Hijmans et al. 2013); this procedure resulted in a reduced predictor set that included only important variables. Habitat thresholds were identified using BRT partial dependence plots, which assess the marginal effect of each predictor on the response, while holding all other predictors constant (Friedman 2001). We defined habitat threshold values by the first abrupt change in slope (i.e. distinct "breakpoint" in marginal effect) along a gradient of predictor values (Cutler et al. 2007, Ficetola and Denoel 2009, Feld 2013).

RESULTS

We surveyed 35 forest stands on Fort Drum during 2012–2013, and found 11 (34%) occupied by territorial Red-headed Woodpeckers in at least one breeding season. We

TABLE 2. Species composition and relative abundance of trees recorded within stand inventory plots and of nest trees used by breeding Red-headed Woodpeckers.

	Available		Nest trees	
Tree species	n	%	n	%
Red oak (*Quercus rubra*)	1,157	38.41	17	70.83
Red maple (*Q. rubrum*)	470	15.60	2	8.33
White oak (*Q. alba*)	316	10.49	2	8.33
Pitch pine (*Pinus rigida*)	278	9.23		
White pine (*P. strobilus*)	249	8.27		
Red pine (*P. resinosa*)	150	4.98	1	4.17
Gray birch (*Betula populifolia*)	108	3.59		
Black cherry (*Prunus serotina*)	100	3.32		
Bigtooth aspen (*Populus grandidentata*)	98	3.25		
Paper birch (*B. papyrifera*)	26	0.86		
Eastern hemlock (*Tsuga canadensis*)	22	0.73		
Scots pine (*Pinus sylvestris*)	11	0.37		
Pin cherry (*Prunus pensylvanica*)	8	0.27		
Eastern cottonwood (*Populus deltoides*)	7	0.23	2	8.33
Quaking aspen (*P. tremuloides*)	6	0.20		
American beech (*Fagus grandifolia*)	3	0.10		
Yellow birch (*B. alleghaniensis*)	3	0.10		
Total	3,012		24	

located 19 nests in 2012 and 11 nests in 2013 for a total of 30 Red-headed Woodpecker nest trees over the course of the study; we retained 24 nests for use in analyses because 6 nests were renest attempts (after nest failure) within the same year.

Nest Cavity Characteristics
Red-headed Woodpeckers nested in 5 tree species, including red oak (71%), white oak (8%), red maple (8%), eastern cottonwood (*P. deltoides*; 8%), and red pine (4%) (Table 2). Nests were located in both limbs (54%) and boles (46%) of trees, and in live (13%) and dead (87%) wood. Cavities were typically placed high in trees, averaging 10.1 m ± 0.68 SE from the ground. Red-headed Woodpecker nest cavities faced north (25%) and east (21%) more often than other directions, but we found too few unoccupied cavities to test for selectivity.

Scale-dependent Nest Habitat Thresholds
   Nest tree thresholds. The simplified (final) model evaluating nest tree thresholds indicated excellent discrimination efficiency (cross-validated AUC: $\bar{x} = 0.90 \pm 0.35$ SE), and retained 3 predictor variables that best discriminated Red-headed Woodpecker nest trees. Red-headed Woodpecker nest tree selection was most influenced by tree (1) decay class, (2) cumulative dead limb length, and (3) dbh (Table 3). Partial dependence plots indicated strong (i.e. an abrupt change in slope) nest tree thresholds related to each of these variables (Figure 2). Individual trees become suitable for use as Red-headed Woodpecker nest trees when they exceed a decay class threshold value corresponding to trees with ≥33% decadent canopies. Nest tree thresholds also existed for trees with cumulative dead limb lengths of ≥4 m and dbh of ≥34 cm (Figure 2).

   Forest patch thresholds. Our simplified model evaluating forest patch thresholds had acceptable cross-validated discrimination efficiency (cross-validated AUC: $\bar{x} = 0.80 \pm 0.56$ SE). At the forest patch scale (within 0.04 ha of the nest tree), Red-headed Woodpecker nest habitat selection was most influenced by (1) cumulative dead limb

TABLE 3. Relative influences of habitat variables on nest tree selection by Red-headed Woodpeckers as derived from boosted regression tree (BRT) models. Relative influence values are given for both fully parameterized (global) and simplified (final) models. Means and standard errors (SE) are also presented. See Table 1 for description of habitat variables.

Variable	Relative % influence		Nest tree		Available tree	
	Full	Simplified	Mean	SE	Mean	SE
Tree decay class	45.50	48.63	4.21	0.39	1.82	0.17
Cumulative dead limb length (m)	27.39	33.08	11.25	2.08	3.04	1.00
Tree dbh (cm)	16.17	18.30	46.79	3.22	31.95	2.29
No. of dead limbs	4.08		4.04	0.77	1.08	0.29
Tree height (m)	3.11		12.69	0.70	11.81	0.37
Tree top condition	1.60					
Tree species	1.19					
Tree state	0.55					
Tree bark	0.39					
Limb tree	0.00					

length, (2) woody understory height, (3) mean tree dbh, and (4) density of large trees ($\geq$30 cm dbh; Table 4). The cumulative dead limb length threshold (Figure 3) corresponded to a minimum of 17 m per 0.04 ha. Woody understory vegetation height had a negative influence on Red-headed Woodpecker forest patch selection, and suitability decreased once woody understory vegetation exceeded a threshold height of 12 cm (Figure 3). Forest patch thresholds were also related to a minimum mean tree dbh of 30 cm, and for a minimum large tree density of 4 per 0.04 ha.

   Forest stand thresholds. Our simplified model comparing structural characteristics of occupied and unoccupied forest stands achieved acceptable discrimination efficiency (cross-validated AUC: $\bar{x} = 0.85 \pm 0.06$ SE). Red-headed Woodpeckers selected forest stands based on mean tree decay and woody understory height (Table 5). Forest stand thresholds corresponded to minimum mean tree decay (trees on average had $\geq 1\%$ crown decay) and a maximum understory height of 12 cm (Figure 4).

DISCUSSION

Red-headed Woodpeckers are known to select habitats characterized by large, sparsely distributed trees and open understories (Smith et al. 2000), and we identified nest habitat thresholds that correspond to these structural attributes. In northern New York, Red-headed Woodpeckers consistently selected for dead limbs, open understories, and decadent trees at multiple spatial scales (Figures 2–4). Given the requirement of soft wood for cavity excavation, it was not surprising that Red-headed Woodpeckers, weak primary excavators (Jackson 1976), selected large and decadent nest trees. Of interest, however, was their selection of nest trees that were in partial states of decline (partial crown decay), and not necessarily for severely decayed snags (only bole remains). This finding supports a growing body of literature demonstrating the importance of declining, but not dead, trees for primary excavators (Martin et al. 2004, Blanc and Martin 2012). For example, primary excavators are known to place cavities in decayed
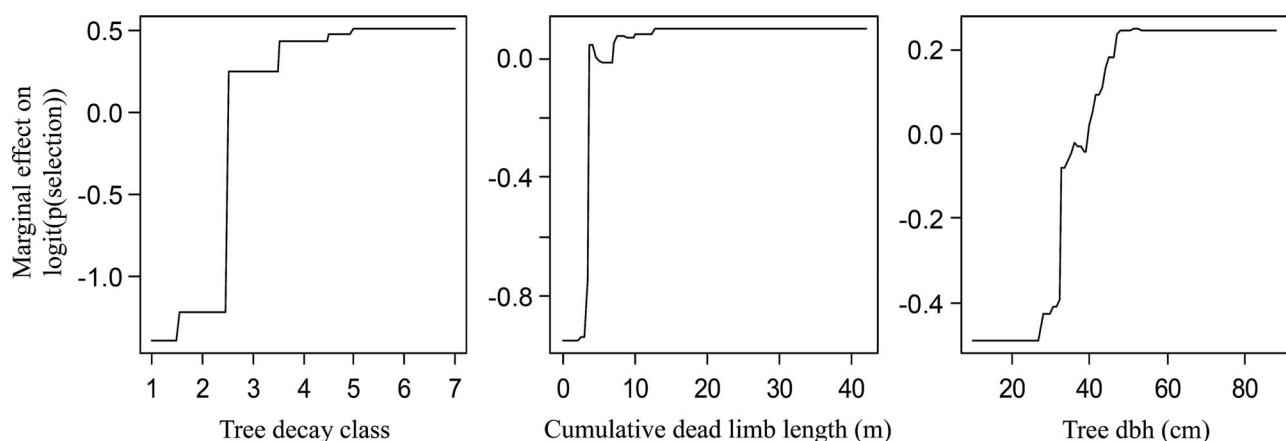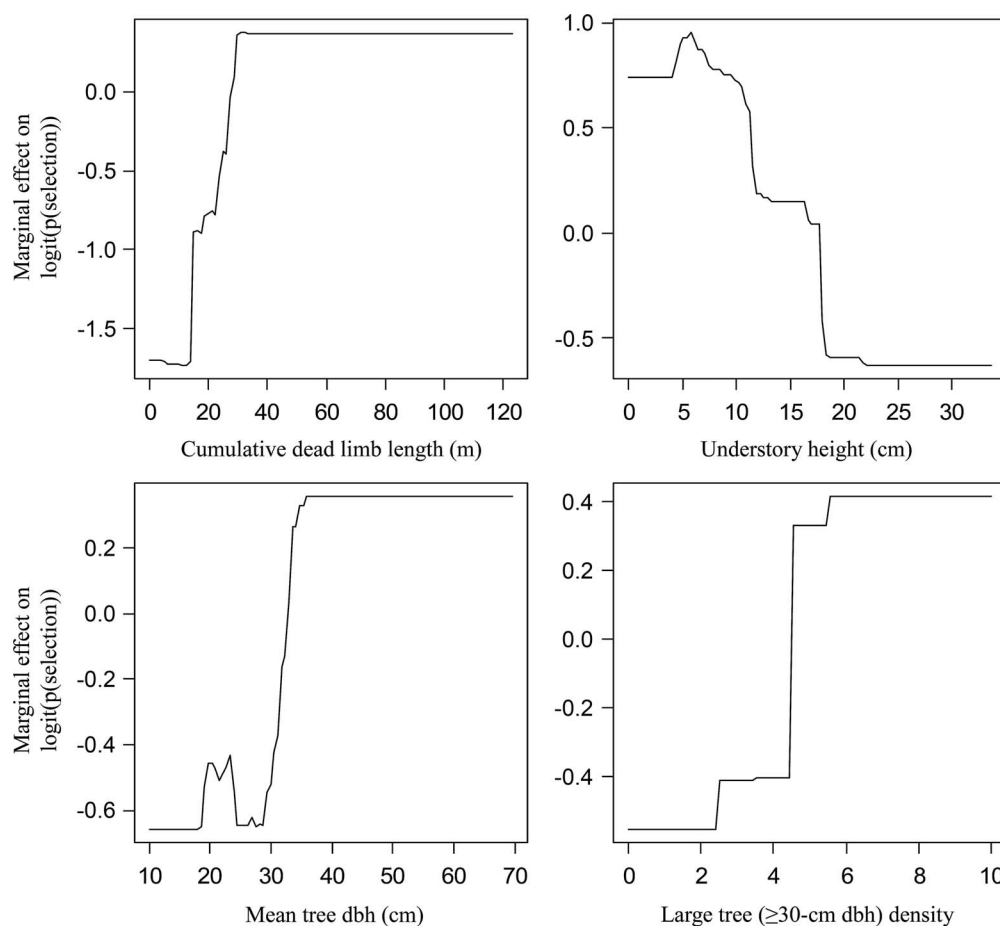

FIGURE 2. Partial dependence plots indicating the marginal effect of nest tree characteristics on the probability of nest tree selection by Red-headed Woodpeckers. Nest tree thresholds were identified by the first abrupt change in marginal effect along a habitat gradient. See Table 1 for description of habitat variables.

TABLE 4. Relative influences of habitat variables on forest patch selection by Red-headed Woodpeckers as derived from boosted regression tree (BRT) models. Relative influence values are given for both fully parameterized (global) and simplified (final) models. Means and standard errors (SE) are also presented. See Table 1 for description of habitat variables.

Variable	Relative % influence		Used		Available	
	Full	Simplified	Mean	SE	Mean	SE
Cumulative dead limb length (m)	23.22	36.95	30.33	3.87	18.64	3.47
Understory height (cm)	11.94	23.30	9.30	1.49	13.79	1.41
Mean tree dbh (cm)	9.92	22.19	32.10	3.03	23.17	1.08
Large tree density	11.49	17.57	5.50	0.47	3.38	0.30
Mean tree decay class	12.59		2.28	0.16	1.92	0.09
Medium tree density	10.67		2.87	0.62	5.14	0.56
Dead limb tree density	6.83		4.45	0.46	3.10	0.31
Canopy height (m)	4.52		12.43	0.68	10.99	0.27
Small tree density	3.67		7.79	2.45	9.24	1.81
Snag density	2.40		2.04	0.56	1.14	0.21
Canopy cover (%)	1.71		75.36	3.71	70.45	2.83
Dead limb density	0.66		11.92	1.62	7.46	0.95
Total tree density	0.39		16.17	2.77	17.76	2.00

FIGURE 3. Partial dependence plots indicating the marginal effect of forest patch characteristics on the probability of forest patch selection by Red-headed Woodpeckers. Forest patch thresholds were identified by the first abrupt change in marginal effect along a habitat gradient. See Table 1 for description of habitat variables.

TABLE 5. Relative influences of habitat variables on forest stand selection by Red-headed Woodpeckers as derived from boosted regression tree (BRT) models. Relative influence values are given for both fully parameterized (global) and simplified (final) models. Means and standard errors (SE) are also presented. See Table 1 for description of habitat variables.

Variable	Relative % influence		Used		Available	
	Full	Simplified	Mean	SE	Mean	SE
Mean tree decay class	67.90	73.90	1.95	0.11	1.45	0.08
Understory height (cm)	16.00	26.00	12.34	1.70	15.78	1.73
Mean tree dbh (cm)	6.90		24.53	2.00	20.93	2.09
Small tree density	2.60		8.91	3.45	12.89	2.67
Sapling density	1.60		14.75	3.48	20.79	4.74
Medium tree density	1.20		5.00	0.88	5.42	0.97
Total tree density	0.80		17.59	3.94	21.48	3.38
Dead limb tree density	0.80		3.29	0.54	2.20	0.39
Stand area (ha)	0.80		12.54	2.34	7.38	1.44
Cumulative dead limb length (m)	0.40		20.25	5.14	11.10	2.29
Dead limb density	0.40		8.03	1.61	4.88	0.83
Canopy height (m)	0.20		10.93	0.44	10.55	0.46
Large tree density	0.20		3.68	0.39	3.17	0.49
Snag density	0.10		1.22	0.35	0.73	0.23
Shrub density	0.00		22.36	5.01	26.54	6.63
Canopy cover (%)	0.00		71.47	4.26	71.62	4.84

portions (typically limbs) of otherwise live trees in North America (Sedgwick and Knopf 1990, Li and Martin 1991, Newlon and Saab 2011, Blanc and Martin 2012), Europe (Smith 1997, Butler et al. 2004), and South America (Cockle et al. 2011). When selecting nest sites and cavity locations, primary excavators must balance ease of excavation (decadent wood) with other factors affecting reproductive success (e.g., predation risk and interspecific interactions) and thus may not perceive severely decayed snags as the highest quality nest structures. Over 54% of Red-headed Woodpecker nests on Fort Drum were excavated in dead limbs (21% in dead limbs of live trees) and their propensity to select this nest location (as opposed to the bole of a tree) may explain why partially decayed trees were suitable nest sites. Furthermore, nest survival of this population is positively related to vegetative

cover surrounding the nest cavity (Berl et al. 2014). Therefore, Red-headed Woodpecker pairs may have excavated nest cavities in dead limbs of partially decayed trees (i.e. those with live vegetation remaining) in an effort to increase nest survival.

At the forest patch and forest stand scales, Red-headed Woodpeckers identified suitable nesting habitat based on cumulative dead limb length, understory height, and mean tree decay—a measure of stand decadence. Stand decadence is a key factor affecting Red-headed Woodpecker selection of nesting habitat in both the core (King et al. 2007) and periphery (this study) of their range, and thus provides range-wide evidence to manage for decadent tree resources. In addition, Red-headed Woodpeckers were recently shown to numerically respond to experimental snag creation (Kilgo and Vukovich 2014), suggesting that
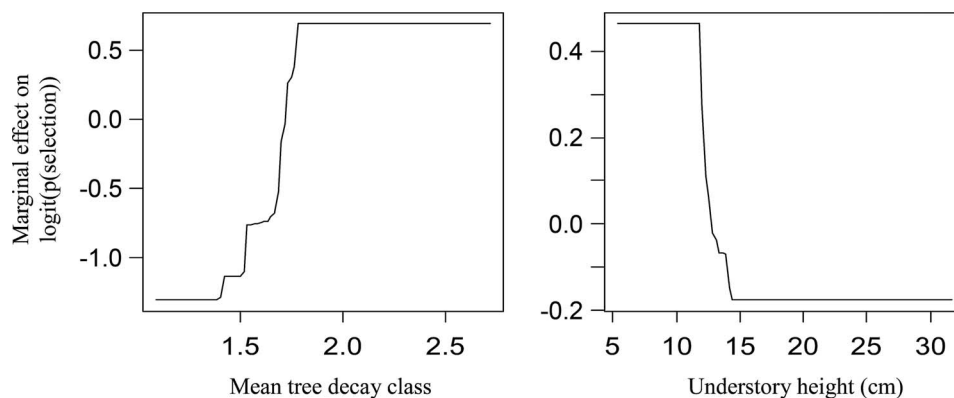
FIGURE 4. Partial dependence plots indicating the marginal effect of forest stand characteristics on the probability of forest stand selection by Red-headed Woodpeckers. Forest stand thresholds were identified by the first abrupt change in marginal effect along a habitat gradient. See Table 1 for description of habitat variables.

the availability of decadent trees (i.e. snags and partially decayed trees) is an important contributor to local abundance. Therefore, management practices that artificially increase the abundance of decadent trees (e.g., tree or limb girdling) will likely increase available nesting habitat for this species (Kilgo and Vukovich 2014). In particular, girdling of large limbs within otherwise live trees, while potentially more challenging than girdling whole trees, may be an effective management strategy that increases the abundance of a critical resource. In addition to providing suitable cavity structures, dead limbs on trees surrounding the nest site can be important roosting and drumming resources (Sedgwick and Knopf 1990, Rodewald et al. 2005), and the length of these limbs can influence their suitability as perching sites during foraging bouts (Reller 1972, Frei et al. 2013). Furthermore, creating dead limbs within otherwise live trees may improve nest success as these trees maintain favorable vegetative cover (Berl et al. 2014).

Red-headed Woodpeckers also selected nest habitat with short (<12 cm) woody understory heights. Selection against woody understory vegetation was likely related to Red-headed Woodpeckers' propensity to ground forage for hard mast and insects during late spring and early summer (J. Berl, personal observation). Dense mats of woody lowbush blueberry and shade-tolerant tree regeneration within oak woodlands on Fort Drum may have restricted the ability of individuals to ground forage and thus resulted in their selection of nest habitat with minimal woody ground cover. When identifying suitable nest habitat, Red-headed Woodpecker pairs must select territories of appropriate size and configuration to ensure that both nest substrate (i.e. decadent trees) and suitable foraging habitat (i.e. open understories) requirements are met (sensu Tingley et al. 2014). Frei et al. (2013) found Red-headed Woodpeckers to select forested woodlots in southern Ontario that maximized foraging conditions (forest openness and length of dead limbs) but not nesting resources. It appears that on Fort Drum breeding pairs attempted to maximize nesting and foraging resource requirements by selecting habitats that contained both decadent trees (cavity structures) and had minimal ground cover (foraging habitat). King et al. (2007) suggested that when selecting nesting habitat, stand-level tree decadence (macrohabitat selection) likely supersedes the importance of individual nest trees (microhabitat selection) for nesting pairs. We did not test for interactions of variables among spatial scales, and thus cannot address the extent to which coarse-scale nest habitat selection influenced fine-scale selection, and vice versa. However, habitat cues at multiple spatial scales can affect an individual's selection of a particular nest site (Johnson 1980). Thus, while our results do not directly complement the inference of King et al. (2007), they do highlight the relative importance of both

nesting habitat and foraging habitat at multiple spatial scales.

The majority of available Red-headed Woodpecker habitat types (e.g., grassland and woodlot edges, savanna, and parklands) in the northeastern and midwestern United States have been permanently altered because of their suitability for development or conversion to agriculture (Lorimer and White 2003). Specifically, we hypothesize that two key land-use changes have reduced the distribution of suitable habitats in this region. In recent decades, forest management practices such as short-rotation harvests and firewood cutting have reduced the distribution and quality of highly decayed forest stands. These practices may have depleted decadent tree resources below threshold levels required by nesting Red-headed Woodpeckers (King et al. 2007). Secondly, elimination of disturbance regimes (e.g., fire suppression) that maintain open understories in oak woodlands has contributed to the proliferation of shade-tolerant tree species in oak-canopy forests (Nowacki and Abrams 2008). Consequently, overabundance of shade-tolerant tree regeneration (e.g., red maple) in formerly suitable habitat patches may have increased under- and mid-story vegetation beyond threshold levels that are acceptable for Red-headed Woodpeckers. Interestingly, military training activities (e.g., tracked-vehicle maneuvering and troop bivouacking) on Fort Drum probably have maintained suitable nesting conditions by limiting understory vegetation within oak woodlands. Consequently, similar activities may prove useful in managing habitat for Red-headed Woodpeckers in other areas.

Ecological Implications of Nest Habitat Thresholds

The existence of threshold responses to habitat by Red-headed Woodpeckers suggests that a lack of suitable nesting habitat may be limiting population growth. This is particularly relevant near the periphery of the species' range where populations have precipitously declined. To some extent, this can be expected because resources are typically more limited near the periphery of a species' range (Brown 1984). However, ecological theory predicts that, although the distribution of suitable habitat diminishes towards range limits, small patches of high-quality habitat may remain (Sexton et al. 2009). In New York, several local populations of Red-headed Woodpeckers have gone extinct in recent decades (McGowan and Corwin 2008), such that remnant subpopulations are small and patchily distributed—presumably persisting on the remaining habitats of highest quality. The existence of nest habitat thresholds in remnant populations (i.e. Fort Drum's population) may therefore provide a possible explanation to the long-term population declines observed in this region, given that suitable habitats must meet or exceed multi-metric and multi-scale threshold criteria. Subse-

quently, it seems plausible that minor changes (for a particular habitat metric or spatial scale) to formerly suitable habitat patches resulted in a "change of state," or rapid transition from suitable habitat to unsuitable habitat (Lindenmayer and Luck 2005).

Red-headed Woodpeckers appear to exhibit threshold responses to nest habitat in both the core and periphery of their range, yet the ecological processes perpetuating this response remain unknown. One potential explanation for threshold responses in primary excavators is that competition for a limited resource constrains an individual's selection of habitat. When suitable nest sites are limited, inter- and intra-specific competition is expected to constrain the selection of nest habitat by members of a cavity-nesting community (Bull et al. 1986, Martin and Eadie 1999, Martin et al. 2004) and these interactions can vary with habitat quality and composition (Robles and Martin 2013, Robles and Martin 2014). For example, in longleaf pine (*P. palustris*) forests of the southeastern United States, Red-headed Woodpeckers are considered a dominant cavity excavator and are known to partition their nest habitat with other cavity nesters (Blanc and Walters 2008). Within oak woodlands of the northeastern United States, Red-headed Woodpecker selection of nesting habitat is likely shaped by other members of a robust cavity-nesting bird community that includes 5 other woodpeckers (Northern Flicker [*Colaptes auratus*], Hairy Woodpecker [*Picoides villosus*], Downy Woodpecker [*P. pubescens*], Yellow-bellied Sapsucker [*Sphyrapicus varius*], and Pileated Woodpecker [*Dryocopus pileatus*]), 3 weak excavators (White-breasted Nuthatch [*Sitta carolinensis*], Red-breasted Nuthatch [*S. canadensis*], and Black-capped Chickadee [*Poecile atricapillus*]), and 5 secondary cavity nesters (Great Crested Flycatcher [*Myiarchus crinitus*], Eastern Bluebird [*Sialia sialis*], American Kestrel [*Falco sparverius*], European Starling [*Sturnus vulgaris*], and House Wren [*Troglodytes aedon*]). In an attempt to reduce direct interference competition from other cavity excavators (e.g., Northern Flickers), Red-headed Woodpeckers may have narrowed their niche breadth, resulting in a truncated (threshold) selection response. Additionally, cavity excavators can alter their habitat selection and behavior to reduce competition (or nest usurpation) from dominant secondary cavity nesters, such as the European Starling or American Kestrel (Ingold 1994). Consequently, the thresholds that we observed may have resulted from interspecific niche partitioning (and narrowing) among competitors for a limited number of suitable nest sites. Although we did not identify any instances of interspecific nest usurpation on Fort Drum, we did document an attempted conspecific nest usurpation (Berl et al. 2013), which indicates that, to some extent, suitable cavity substrates are a limited resource on the installation.

Conclusions

Habitat management and restoration remain the most widely used conservation strategies implemented by land and resource managers, and identification of habitat thresholds can be an effective management tool for imperiled wildlife populations (Huggett 2005, Lindenmayer and Luck 2005, Ficetola and Denoel 2009). We found strong evidence for scale-dependent and multi-metric nest habitat thresholds for a peripheral population of Red-headed Woodpeckers that can provide objective nest habitat requirements and inform management decisions. Red-headed Woodpeckers consistently selected for dead wood, large trees, and open understories at multiple spatial scales, and habitat management for Red-headed Woodpeckers in the northeastern United States should attempt to meet or exceed these minimum (or maximum) nest habitat thresholds. Although these thresholds are useful from a management perspective, greater evaluation of the ecological factors underpinning the responses we observed are necessary to fully understand the extent to which this species–habitat relation is shaped by other members of the cavity-nesting community.

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