Habitat Characteristics of Active and Abandoned Red-Cockaded Woodpecker Colonies

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ABSTRACT. Active red-cockaded woodpecker (Picoides borealis) *colonies in the Piedmont of Georgia are mature pine stands* (mean age = 87 ± 1 yr old) *with relatively* sparse *midstories (mean basal area = 31 ± 3 ft²/ac). Active and abandoned colony sites have similar overstory characteristics, but midstories are significantly denser in abandoned colony sites* (mean *basal* area = 56 ± 3 *ft²/ac). Previous studies* have *focused on the effect of hardwoods in the midstory, but we found that increases in both pine and hardwood midstory density are associated with colony abandonment. A logistic regression model based on field data suggests that the probability of a colony becoming abandoned increases considerably when midstory basal area is >30 ft²/ac. To maintain red-cockaded woodpecker populations,* manag*ers should keep midstory basal area in colonies below 25 ft²/ac. Treatments should be applied to entire stands* and *not just around individual cavity trees.*

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The endangered red-cockaded woodpecker is endemic to the pine forests of the South. If the red-cockaded woodpecker is to recover to threatened or nonendangered status, currently occupied habitats must be managed to forestall further population declines, and new habitat must be provided to promote population expansion. Red-cockaded populations are limited by available nesting habitat (USFWS 1985). Because the woodpeckers require old-growth living pine for nesting habitat, new habitats become available slowly over time. Thus, the need for conservation of existing habitat is amplified.

One factor threatening existing red-cockaded habitats is natural habitat deterioration as hardwoods develop in pure pine stands during plant succession (USFWS 1985). Beckett (197 1) suggested that red-cockaded woodpeckers would abandon their cavity trees if the hardwood midstory reached the height of cavity entrances. Most authorities accept that opinion. Jackson (1978) speculated that pine stands that were located on moist sites and had well-developed hardwood midstories might provide better habitat for larger woodpeckers that enlarge and usurp cavities occupied by red-cockadeds. Eliminating or reducing hardwood midstory in red-cockaded woodpecker nesting habitat is recommended because it may minimize interspecific competition for cavities. However, the relationship between hardwood midstory density and suitability of stands as habitat for red-cockadeds is not well understood.

Grimes (1977) and Lennartz et al. (1983) described hardwood composition in active red-cockaded colonies (i.e., the aggregations of cavity trees used by families of red-cockaded woodpeckers), and Locke et al. (1983) and Van Balen and Doerr (1978) contrasted hardwood density in active colonies with hardwood density in nonoccupied pine stands selected at random on the same forests. In all studies hardwood basal area in active colonies was relatively low (3.7-20 ft²/ac), and Locke et al. (1983) and Van Balen and Doerr (1978) found higher hardwood basal areas (25-30 ft²/ac) in stands not occupied by red-cockadeds. Although these studies suggest that the density of hardwoods may be a primary factor in determining suitability, it is possible that suitability is determined by other factors. For example, it is well established that red-cockaded woodpeckers select trees infected with heartrot (*Phellinus pini*) to excavate their cavities (Jackson 1977, Conner and Locke 1982, Hooper 1988). Because neither Locke et al. (1983) nor Van Balen and Doerr (1978) determined whether unoccupied habitats contained pines with heartrot, they did not exclude the possibility that the absence of birds was related to the lack of suitable cavity trees.

To determine more directly whether stand structure in general, and hardwood density in particular, influence suitability of habitat for red-cockaded woodpeckers, we compared stand structure and density in active and inactive red-cockaded colonies. Because inactive colonies by definition contain cavity trees once occupied by red-cockadeds, inferences about the influence of stand structure and density on habitat suitability were not confounded by uncertainty about cavity tree availability. Recently, other investigators have also taken this approach. Kalisz and Boettcher (1991) compared habitat surrounding active and inactive red-cockaded woodpecker colonies on the northern edge of the species range and Conner and Rudolph (1989) followed active colonies in Texas over a 4- to 6-year period and compared habitat of colonies that became inactive to those that remained active.

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METHODS

The study was conducted primarily on the Piedmont National Wildlife Refuge and the Hitchiti Experimental Forest in Jasper and Jones Counties, GA. The two properties are contiguous and support 37 clans (i.e., family groups) of red-cockaded woodpeckers (Lennartz and Metteauer 1986). To increase our sample of inactive colonies, we also sampled 6 inactive colonies on the Oconee National Forest (Jasper and Putnam Co., GA) and 2 inactive colonies on the Bishop F. Grant State Forest (Putnam Co., GA). The Oconee National Forest is on the northern border of the Piedmont Refuge and the Bishop F. Grant Forest is approximately 35 mi from the Refuge. All forests include an array of pine, pine-hardwood, and hardwood habitats typical of the Piedmont province. Loblolly pine (*Pinus taeda*) is the predominant pine species.

An intensive study of the population dynamics of the Piedmont-Hitchiti population was initiated in 1983 (Lennartz and Heckel 1987). The researchers visited all groups of cavity trees; classified each tree as active (signs of fresh chipping by woodpeckers) or inactive; captured and color-marked the resident woodpeckers; determined which birds were associated with which groups of trees; and monitored nesting success. Groups of trees with active, freshly chipped trees and a resident pair of woodpeckers were considered active colonies. Groups of trees with no fresh chipping or signs of activity and located at least ¼ mi distant from active trees were considered inactive colonies. To assure that all trees were located and colonies correctly classified, a circular area of 1500 ft radius around each colony was systematically searched for cavity trees that might have been missed by forestry crews or that had been excavated by the woodpeckers subsequent to the last compartment prescription. In two active colonies, the cavity trees were distributed in two distinct groups 200 to 400 yd apart. Because stand conditions in the isolated groups differed, we treated the groups as four colonies for sampling purposes. Data were collected during winter 1984. At least four of the colonies became inactive between 1979 and 198 1, but because detailed records on colonies were not kept prior to 1979, we do not know when the other colonies became inactive.

We determined the vegetation composition and structure in 34 active and 19 inactive colonies. Five points were established in the center of each colony. One of these points was established at the intersection of the lines connecting the easternmost and westernmost cavity trees and the northernmost and southernmost cavity trees. The other four points were located 50 yd from the center in each of the cardinal directions. Each point was the center of a lo-factor prism plot for sampling trees. We also randomly selected two cavity trees—one active and the other inactive—within each active colony and established a O.Ol-ac circular plot adjacent to each of these trees. Each plot center was located 12 ft from the cavity tree in the direction the cavity faced. These plots allowed us to compare midstory conditions around individual cavity trees within colonies as well as among colonies.

At each point a prism sample was taken of all trees 1 in. dbh and larger. The species, dbh, status (living or dead), and crown position (midstory or overstory) of each sample tree was recorded. Hardwoods were identified to species only at the center sample point. The height of the tallest hardwood tree within each prism plot was measured to provide an estimate of the maximum height of the midstory. The heights of five randomly selected hardwood stems at the center point were measured to provide an estimate of average midstory height. Ages of all cavity trees and four dominant or codominant trees around the center sample point were determined by examining increment cores. On the circular plots adjacent to individual cavity trees, we sampled only midstory trees. Each was categorized as hardwood or pine and living or dead, and its dbh was recorded. Each colony stand was also characterized by several site variables. These variables were treatment history, major treatment influence, proximity to permanent openings, and land form. Treatment histories (e.g., thinning, burning) were determined from administrative records and from visual evidence of disturbance. For stands that had received multiple treatments, we estimated which treatment had most likely had the major influence on stand structure. Proximity to permanent openings and the type of openings were determined from aerial photos. Each colony site was classified as floodplain, narrow floodplain, stream terrace, side slope, ridge, or upland flat (USFS 1972).

The variables used to compare active and abandoned colonies were basal area and number of stems/ac for the overstory, midstory, and total stand; maximum and average midstory height; overstory height; treatment history; proximity to openings; and land form. Only midstory basal area and number of stems/ac were used to compare the habitat adjacent to active and inactive cavity trees. Values for pines and hardwoods were analyzed separately and in combination.

Differences between midstory characteristics in areas around active and inactive trees were tested with univariate t-tests. Stand conditions in active and abandoned colonies were also compared with univariate t-tests. Possible correlations between colony activity and land form were tested with a chi-square test of independence.

Logistic regression analysis was used to determine which set of stand variables best predicted abandonment of colony sites. The logistic regression model describes a relationship between a set of independent variables and a binary variable Y, where Y = 1 for stands classified as active colonies and Y = 0 for stands classified as inactive colonies. The fitted model is:

$$p = 1/(1 + \exp(-b_0 - b_1x_1 - b_2x_2 - \ldots - b_kx_k)),$$

where

p = predicted probability that Y = 1,

x_i = ith independent variable (i = 1, . . . , k),

b_0 = estimated intercept parameter, and

b_i = estimated regression coefficient for x_i.

The predicted value p is interpreted as the probability that a stand with the attributes x_i (i = 1, 2, . . . , k) will provide a suitable habitat for hosting an active colony. The SAS procedure LOGIST (SAS Institute Inc. 1983) was used to fit the logistic model to our data. This procedure computes maximum likelihood estimates for model parameters using the Newton-Raphson method.

A stepwise selection procedure was used to screen 22 variables including the number of stems/ac, basal area, average midstory height, overstory height, and stand age (see Table 2). Chi-square tests for including and retaining individual variables in the model at each step were performed at α = 0.15 so we could examine the relationships among several of the variables. Model 1 is the result of the preliminary stepwise procedure. We developed Models 2-4 by substituting, selected variables for those in Model 1. These models were developed to clarify some of the relationships between midstory variables. In the second phase of variable selection the stepwise selection procedure was again applied to all 22 variables, but the chi-square tests for including and retaining variables at each step were performed at α = 0.05. The intention was to select a model with a minimum number of variables for field use. The result of this procedure is Model 5.

We used three criteria to evaluate each model. The first was a fit statistic, R, which is analogous to the multiple correlation coefficient in the normal regression setting. We used the square of this quantity as an indicator of predictive ability, but this criterion used alone is unreliable. The second criterion was the statistic C, the fraction of all possible pairs of Y values in which the higher Y value has the higher predicted value. Values of C near 1 indicate high predictive ability.

LOGIST also computes large-sample approximations for confidence intervals of predicted probabilities. For each model we calculated the half-length of the confidence interval for each predicted value generated by our data. We refer to the distance between the predicted value and the confidence limit as a limit of error (LE) since we can state with 95% confidence that the actual prediction error is within this limit. We averaged these quantities over all observations to obtain the average LE for the model. Average LE is a direct expression of predictive precision.

RESULTS AND DISCUSSION

We found no significant differences between midstory vegetation around active cavity trees and around inactive cavity trees (Table 1). However, stand conditions in active colonies were distinctly different from those in inactive colonies (Table 2). Active colonies had significantly lower total stems/ac (TST), total basal area (TBA), total hardwood basal area (THBA), midstory pine basal area (MPBA), midstory hardwood basal area (MHBA), total midstory basal area (MBA), and midstory stems/ac (MST) than inactive colonies. Differences in TST, TBA, and THBA were related to differences in midstory rather than overstory conditions because overstory stems/ac, overstory basal area, and overstory hardwood basal area did not differ significantly between active and inactive colonies (Table 2).

The logistic regression analysis and the univariate analysis yielded

Table 1. Midstory characteristics (mean ± 1 standard error) adjacent to active and inactive red-cockaded woodpecker cavity trees. No differences between active and inactive trees were statistically significant ($P > 0.05$).

Habitat parameters	Active trees	Inactive trees
Pine stemslac	193 ± 71	181 ± 53
Hardwood stemslac	371 ± 66	370 ± a2
Total stemslac	564 ± 96	552 ± 85
Pine BA (ft²/ac)	13 ± 5	17 ± 5
Hardwood BA (ft²/ac)	26 ± 6	25 ± 5
Total BA (ft²/ac)	39 ± 6	42 ± 7

Table 2. Stand characteristics (mean ± 1 standard error) of active and abandoned red-cockaded woodpecker colonies.'

Habitat variables	Abbrev. name	Active colonies		Inactive colonies
Stand age	AGE	87 ± 1		83 ± 3
Cavity tree age		92 ± 1		97 ± 2
Total pine stemslac	TPST	232 ± 56		282 ± 40
Total hardwood stems/ac	THST	319 ± 66		407 ± 65
Total stemslac	TST	551 ± 84	*	769 ± 66
Total pine BA (ft²/ac)	TPBA	67 ± 4		74 ± 5
Total hardwood BA (ft²/ac)	THBA	21 ± 3	*	33 ± 4
Total BA (ft²/ac)	TBA	88 ± 4	*	108 ± 5
Overstory pine stems/ac	OPST	50 ± 6		40 ± 4
Overstory hardwood stems/ac	OHST	2 ± 1		3 ± 1
Overstory stems/ac	OST	53 ± 7		43 ± 4
Overstory pine BA (ft²/ac)	OPBA	55 ± 3		40 ± 4
Overstory hardwood BA (ft²/ac)	OHBA	2 ± 1		3 ± 1
Overstory BA (ft²/ac)	OBA	57 ± 3		52 ± 4
Midstory pine stems/ac	MPST	181 ± 56		242 ± 39
Midstory hardwood stems/ac	MHST	317 ± 65		484 ± 65
Midstory stems/ac	MST	498 ± 84	*	726 ± 64
Midstory pine BA (ft²/ac)	MPBA	12 ± 2	*	26 ± 3
Midstory hardwood BA (ft²/ac)	MHBA	18 ± 2	*	30 ± 3
Midstory BA (ft²/ac)	MBA	31 ± 3	*	56 ± 3
Maximum midstory height (ft)		42 ± 2		46 ± 2
Average midstory height (ft)	MHT	28 ± 1		26 ± 1
Distance to opening (yd)	DIST	200 ± 28		303 ± 58
Overstory height (ft)	OHT	92 ± 2		86 ± 2

[1] * denotes a statistically significant difference ($P \leq 0.05$).

similar results (Table 3). Although the original screening process was coarse ($\alpha = 0.15$), only 3 of the 22 variables were selected in Model 1: MBA, TST, and MHT. None of the 19 remaining variables, when adjusted for these 3, passed the selection test. The three evaluation criteria for Model 1 suggest that this set of variables is strongly correlated with habitat suitability. In a normal regression setting $R^2 = 44$ is not especially impressive, but the corresponding chi-square value for total regression ($\chi^2 = 27.88$, $df = 3$, $P < 0.0001$) is highly significant. The average LE for Model 1 is 18 percentage points-that is, our predicted value is within 18 percentage points of the true value 95% of the time. The fraction of concordant values, C, is also quite high. Of all possible pairs of Y values in our data set, the higher value was associated with a higher predicted value 93% of the time.

Since TST = OST + MST, TST is nearly perfectly correlated with MST ($r = 0.99$). Thus, we decided to fit Model 2 with only midstory variables, replacing TST in Model 1 with MST. Neither C or *LE* changed and R^2 decreased by only 2 percentage points (Table 3). Thus, we are able to restrict our attention to midstory variables.

We fitted Model 3 to see the results of separating midstory stems/ac and basal area into pine and hardwood components. The predictive capability of Model 3 is not substantially different from that of Model 2 (Table 3). Both MPST and MHST were positively but weakly correlated with colony activity ($\chi^2 = 2.28$, $P = 0.13$ and $\chi^2 = 3.28$, $P = 0.07$, respectively). In contrast, both pine and hardwood basal area had strong negative associations with colony activity (MPBA: $\chi^2 = 8.77$, $P = 0.003$, MHBA: $\chi^2 = 7.72$, $P = 0.006$). Based on the relative size of the individual chi-square statistics, we see no evidence that midstory pines and hardwoods affect habitat suitability differently. However, basal area is more important than number of stems/ac.

The performance of Model 3 suggested that the midstory stems/ac variables could be eliminated with little sacrifice in predictive capability. This is confirmed with Models 4 and 5. In Model 4, only midstory basal area variables and MHT were entered into the model. While this resulted in a decrease in R^2, *LE* improved slightly and C decreased only a little (Table 3). Both MPBA and MHBA were significant at $P \leqslant 0.0026$, and individual chi-square statistics were nearly equal, providing further evidence that midstory pines and hardwoods have similar effects. Model 5 resulted from the tighter screening procedure (selection and retention based on chi-square tests with a = 0.05). The only independent variable fitted in Model 5 is total midstory basal area (MBA). The calculated values of R^2 and C are slightly lower than those for preceding models, but Model 5 produced the lowest average *LE*. The high predictive ability of this model, as well as its simplicity, suggest that it is an excellent model for field use. This model indicates that colony sites are suitable for red-cockaded woodpeckers at midstory basal areas of less than 25-30 ft^2/ac (Figure 1). Above 30 ft^2/ac, suitability decreases rapidly.

Seventy-two percent of the active colonies were on ridges, 19% were on side slopes, and 9% were on stream terraces. Sixty-five percent of inactive colonies were on ridges and 35% on side slopes. The proportion of active colonies on slopes and ridges did not differ significantly ($\chi^2 = 1.19$, $P > 0.05$) from the proportion of inactive colonies on slopes and ridges. Active colonies generally were not close to permanent openings, and proximities of active and inactive colonies to openings were not significantly different (Table 2).

Ideally, to test the effect of habitat characteristics on colony abandonment, measurements should be taken at the time the colony becomes inactive. However, this is not always possible, as in the present study. Thus, the above analyses were based on the assumption that conditions at the time of sampling were the same as at the time of colony abandonment. Because active and inactive colonies occupied stands of similar age (Table 2) and landform, successional chronologies (in the absence of management) would likely be similar between the two groups. Therefore, differential management of active and inactive sites, if it occurred, would be the most important factor resulting in the violation of the above assumption.

Because of the time and expense, habitat management practices to control midstory are usually restricted to active colonies (Costa and Escano 1989). Therefore, our results may have been biased by differential management of active and inactive colonies. Eighty-five percent of the active colonies had been burned or thinned, but only 41% of the inactive colonies had received such treatments. However, thinning had no significant effect on stand structure (Table 2). In fact, overstory basal area and density tended to be higher in active colonies. Although controlled burns had oc-

Table 3. Regression coefficients' and evaluation criteria for fitted models.

Model	Intercept	MPBA	MHBA	MBA	MPST	MHST	MST	TST	MHT	R^2	C	*LE*
										--------	(%)	--------
1	***-3.915***	***0.0***	***0.0***	***-0.197***	***0.0***	***0.0***	***0.0***	***0.004***	0.375	44	93	18
2	-3.379	0.0	0.0	-0.185	0.0	0.0	0.004	0.0	0.355	42	93	18
3	-2.874	-0.241	-0.154	0.0	0.006	0.004	0.0	0.0	0.330	38	94	22
4	1.928	-0.117	-0.103	0.0	0.0	0.0	0.0	0.0	0.126	31	90	19
5	5.134	0.0	0.0	-0.105	0.0	0.0	0.0	0.0	0.0	34	88	14

[1] A regression coefficient of zero indicates the corresponding variable was not included in the model.

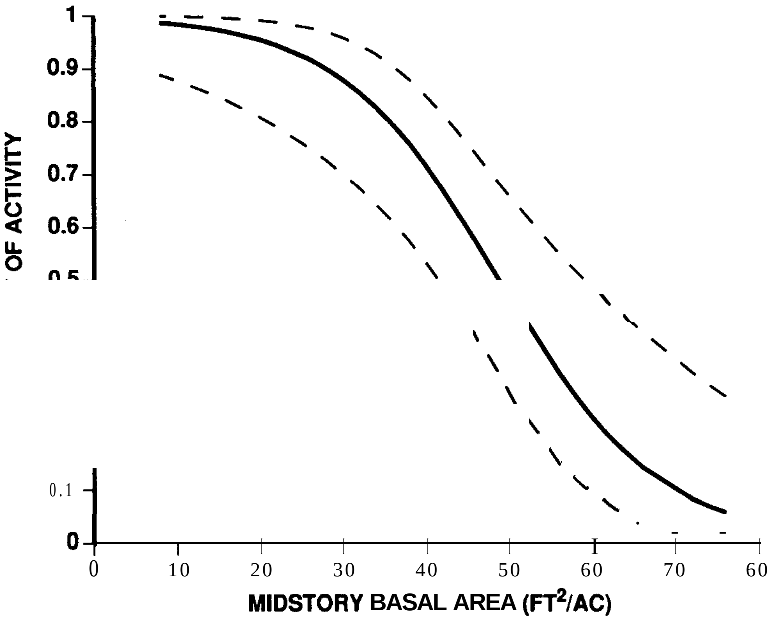

Figure 1. Probabilities of a red-cockaded woodpecker colony remaining active given midstory basal area. Based on a logistic regression model (cx = 0.05). Dotted lines represent 95% confidence limits on the prediction.

curred in 70% of the active colonies versus only 35% of the inactive colonies, burning history was not associated with significant differences in midstory characteristics in either active or inactive sites (Table 4). Further, nonburned active colony sites had significantly lower MPBA (t_{21} = 2.14, $P < 0.05$) and MBA (t_{21} = 3.73, $P < 0.002$) than nonburned inactive sites. Thus, although active colonies received more intense habitat management, these management practices were not sufficient to produce the differences between stand conditions in active and inactive colonies.

Many of the results of this study are consistent with earlier reports of habitat conditions at active red-cockaded woodpecker colony sites (Grimes 1977, Van Balen and Doerr 1978, Lennartz et al. 1983, Locke et al. 1983, USFWS 1985, Conner and Rudolph 1989). Active colony sites in the Piedmont of Georgia can be characterized as mature, moderately stocked pine stands with sparse midstories. Inactive colonies (sites abandoned by red-cockadeds) differed from active colonies primarily in midstory density. Midstory densities were significantly greater in inactive colonies than in active colonies. Our data suggest that once midstory basal area has exceeded 30 ft²/ac, the probability of a colony becoming inactive increases considerably (Figure 1). Earlier studies (Grimes 1977, Van Balen and Doerr 1978, Lennartz et al. 1983, Locke et al. 1983) have suggested that midstory composition influences habitat suitability; our data suggest that the composition of the midstory does not matter. Both pine and hardwood components of the midstory contributed equally to colony abandonment.

Midstory height did not appear to be an important factor in colony abandonment. In fact, we found a slight positive correlation between midstory height and colony activity (Model 1). However, we did not test for differences in midstory height surrounding active and inactive cavity trees and thus did not rule out the possibility that midstory height plays a role in cavity tree abandonment (Beckett 1971).

Although we have demonstrated a negative relationship between midstory basal area and habitat suitability, the proximate factors or direct causes of colony abandonment are still subject to conjecture. It has often been suggested that a dense midstory or the presence of hardwoods in red-cockaded colony sites increases the number of potential competitors and predators in the colonies (Jackson 1978, USFWS 1985, Conner and Rudolph 1989). These predators and competitors include southern flying squirrels (*Glaucomys volans*), rat snakes (*Elaphes* spp.), pileated woodpeckers (*Dryocopus pileatus*), red-bellied woodpeckers (*Melanerpes carolinus*), and red-headed woodpeckers (*M. erythrocephalus*). However, direct evidence linking colony abandonment to competition does not exist at this time. Further, far more data on the relationship between potential predators and competitors of red-cockadeds and habitat structure and composition are needed before we can evaluate the importance of habitat, particularly midstory density, in controlling competition and predation.

Whatever the direct cause or causes of colony abandonment, it is obvious that active sites must be managed and silviculturally treated to support continued occupancy by red-cockadeds. It is our recommendation that midstory vegetation must be kept relatively sparse by means of felling, peri-

Table 4. Midstory characteristics (means ± 1 standard error) of burned and unburned active and abandoned red-cockaded woodpecker colony sites in central Georgia.

Habitat variable	Active colonies: Burned (N = 24)	Active colonies: Unburned (N = 10)	Inactive colonies: Burned (N = 6)	Inactive colonies: Unburned (N = 13)
MPST (stems/ac)	159 ± 61	236 ± 134	241 ± 55	243 ± 53
MHST (stems/ac)	315 ± 89	321 ± 72	400 ± 111	524 ± 80
MST (stems/ac)	474 ± 109	556 ± 121	641 ± 65	767 ± 88
MPBA (ft²/ac)	12 ± 2	13 ± 4	24 ± 3	26 ± 5
MHBA (ft²/ac)	17 ± 3	21 ± 4	29 ± 5	30 ± 5
MBA (ft²/ac)	29 ± 3	34 ± 4	54 ± 4	57 ± 4

odic burning, herbicides, or combinations of these treatments. Vegetation conditions adjacent to individual cavity trees in active colonies did not appear to determine whether the cavity trees were active. Thus, treatments should be on a stand rather than a cavity tree by cavity tree basis. Midstories in inactive colony sites should be treated also. These sites have suitable cavity trees and, with sparse midstories, should provide excellent habitat for population expansion until younger stands reach maturity. □

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