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Estimating cavity tree abundance by stand age and basal area, Missouri, USA

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Abstract

We analyzed cavity tree distribution among Missouri Forest Inventory and Analysis (FIA) plots using the nonparametric classification and regression tree (CART) model and Weibull probability density function (pdf). Fifty-nine per cent (2370) of the 4052 Forest Inventory and Analysis plots (aged 1–160 years) had at least one cavity tree. The overall odds ratio of a plot with cavity trees (odds of a plot having cavity trees/odds of a plot with no cavity trees) across the five survey units of the entire state was 1.4. Three and four disjoint clusters (nodes) which differ significantly in cavity tree distribution were identified by CART using the two most discriminating stand level indicator variables: age and basal area, respectively. Cavity tree density distribution within each cluster was further described by the Weibull pdf.

Cavity tree density per hectares varied considerably among stands (plots) of the same age or density, and the number of cavities for a given size or age class was distributed in an asymmetric form (primarily reverse-J shape). CART partitioning and Weibull fitting, in combination, provide an intuitive way to depict cavity tree distribution (variation) by important stand indicator variables such as age and basal area. This information can help forest managers and planners formulate management guidelines and results can be linked with forest landscape planning efforts, regional inventories, wildlife habitat modeling, and landscape simulation to evaluate or predict the consequences of different management alternatives.
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Keywords: Classification and regression tree; Weibull probability density function; Forest Inventory and Analysis (FIA); Cavity tree; Stand age; Basal area

1. Introduction

Management of cavity trees (both live trees and snags) to meet the habitat requirements of cavity-dependent wildlife is an important topic in resource management and conservation. It is estimated that about one-fourth of northeastern forest wildlife

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species need cavity trees for shelter and other activities (DeGraaf and Shigo, 1985). In Missouri, at least 89 wildlife species depend on cavity trees. Given the dependence of the cavity-nesting birds and other wildlife species on an adequate and continuous supply of cavity trees and snags, management guidelines of snag and cavity trees have been established in Missouri (Titus, 1983) and elsewhere.

An important question facing resource managers and planners is how to incorporate cavity tree goals to formulate management guidelines within a specific forest type and geographic region. Moreover, resource managers and planners are required periodically to evaluate/predict how different management scenarios will impact these goals. Answers to these questions depend on our knowledge about the distribution of cavity trees at multiple spatial scales such as individual trees (species), stands, landscapes, and across forest regions. The cavity resource changes over time, and the ability to anticipate those changes at multiple spatial scales is essential to effective management. Management decisions related to cavity trees also affect other forest products and amenities such as timber production, recreation, and even public safety.

Information on cavity formation processes and abiotic and biotic factors that affect cavity formation has accumulated over the past several decades (Hansen, 1966; McClelland and Frissell, 1975; McClelland et al., 1979; Cline et al., 1980; Mannan et al., 1980; Scott et al., 1980; Van Balen et al., 1982; Carey, 1983; McComb et al., 1986; Sedgwick and Knopf, 1986; Franklin et al., 1987; Healy et al., 1989; Allen and Corn, 1990; Spetich, 1995; Kowal and Husband, 1996; McClelland and McClelland, 1999; Fan et al., 2002; Jensen et al., 2002). But most of these studies concentrated on the distribution of cavity trees or snags on the individual tree or species level. Certain studies, such as Carey (1983), tried to compare the difference of cavity trees at the stand level based on limited data. Little information is available on how cavity trees are distributed among stands of different ages or basal area classes. As shown in previous studies (e.g. Carey, 1983; Fan et al., 2002), cavity development is a relatively rare event governed by stochastic processes that lead to tree injury, decay, or excavations by wildlife. Stand attributes and tree characteristics such as size, decay class, and species only play a partial role in cavity tree development. As a result, there exists a statistically significant but weak association between stand level attributes (e.g. mean dbh) and cavity tree abundance (Carey, 1983). From a statistical perspective, it is difficult to describe this relationship between stand attributes and cavity tree abundance unless a sample large enough to characterize the inherent process of cavity formation is available.

The 1989 Missouri Forest Inventory and Analysis data includes 4052 plots (141,000 trees sampled) and provides a good opportunity to explore the distribution of cavity trees at multiple spatial scales. We previously used these data to characterize the distribution of cavity trees by tree (species) level attributes (Fan et al., 2002). The large number of plots on which cavities were sampled provides a basis for examining stand-level characteristics that are associated with cavity abundance and spatial distribution across larger regions where analyses based on individual tree attributes are impractical to implement. As indicated by Carey (1983), Fan et al. (2002), and others, stand basal area or age is one of the best indicators of cavity tree abundance. Our objective is to quantify the relationship between cavity tree abundance and stand age classes and basal area. This information will help forest managers and planners formulate management guidelines and evaluate management effects on cavity tree resources over time at the forest, landscape, and regional scale.

2. Methods

2.1. Data

We used data from the 1989 Missouri forest inventory, a systematic sample of all timberland in the state (NCFES, 1986; Hahn and Spencer, 1991; Spencer et al., 1992; Miles et al., 2001). Each inventory plot was comprised of 10 subplots spread over approximately 0.4 ha. Trees > 13 cm diameter at breast height (dbh) were sampled with an 8.6-factor angle gauge (m^2/ha) on each subplot and subplots were combined to obtain estimates for the entire plot. For each sampled tree, the size of the largest visible cavity (smallest dimension to the nearest 2.5 cm) and other characteristics such as species, dbh, crown class, and expansion factor were recorded or calculated. For each

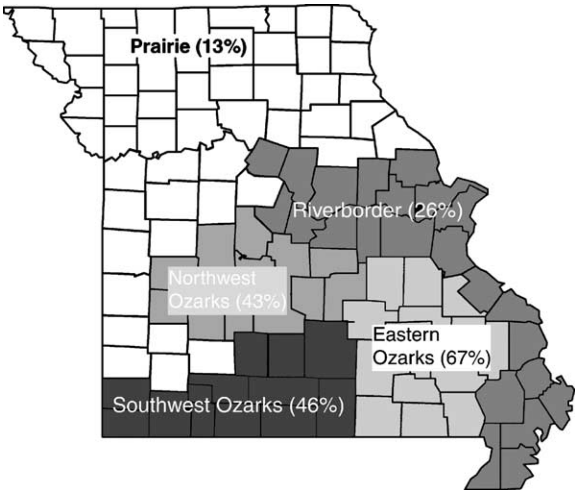

Fig. 1. The five survey units used in the 1989 Missouri state-wide forest inventory to stratify the state into broad ecoregions. Percent of land area in timberland is shown for each region.

Table 1
Distribution of Missouri inventory plots by survey unit, stand size, and age class

	Number of plots	Percentage of plots
Survey unit		
Eastern Ozarks	1154	28
Southwest Ozarks	793	20
Northwest Ozarks	669	17
Prairie	809	20
Riverborder	627	15
Stand size class		
Seedling/sampling	1008	25
Pole	1193	29
Saw-log	1851	46
Stand age class (year)		
1–10	244	6
11–20	726	18
21–30	203	5
31–40	395	10
41–50	574	14
51–60	438	11
61–70	427	11
71–80	358	9
81–90	270	7
91–100	200	5
101–110	108	3
111–120	61	2
121–130	26	1
131–140	12	<1
141–150	7	<1
151–160	9	<1

plot, stand size class (i.e. seedling-sapling, poletimber, and sawtimber) was computed based on stocking by tree size classes. Plots with less than 17% stocking in growing stock trees were classified as non-stocked. Stand age for the predominant size class in the stand was determined from three or more increment corings of trees on or near the plot. Stand age was estimated if a sufficient number of acceptable trees were not available for coring. The cavity tree density (number of cavity trees/ha; a continuous random variable) for each plot over the five survey units of the entire state (Fig. 1 and Table 1) was calculated as the sum of the expansion factors of all sampled trees (live trees or snags) with cavities.

2.2. Statistical analysis

The exploratory data analysis indicated that the probability distribution of cavity tree density at the stand (i.e. plot or per hectare) level generally takes on a reverse-J distribution. Stands with no cavity trees comprised the single largest class, but the probability distribution of cavity tree density changed dramatically from the extremely skewed (e.g. reverse-J shaped) to moderately skewed-to-the-left distributions with an increase of stand age and basal area, the two important indicators of stand development. This change was primarily due to the significant decrease in the proportion of stands with no cavity trees as stand age or basal area increased. This change cannot easily be quantified parametrically. Moreover, the proportion of stands with no cavity trees and its relationship with stand attributes are an important factor to consider in formulating management guidelines. Therefore, we used a two-step modeling approach to study the effect of stand age class and basal area (ba) on cavity tree density and distribution. First, we split the 4052 plots into two groups: those without cavities and those with cavities (represented by 0 and 1, respectively). We then applied the nonparametric classification and regression tree (CART) model (Breiman et al., 1984) to study the effect of stand age class and basal area on the distribution of plots without and with cavity trees and to uncover the most significant thresholds of stand age class and basal area associated with cavity tree presence/absence. We constructed a fully-grown (maximal) classification tree using the gini splitting criterion and derived a set of sub-trees from it by the pruning process. We identified the best CART model based on both the cost-complexity measure and the case number within terminal nodes (should not less than 200 for fitting a Weibull distribution, see below). We also used five-fold cross validation (Steinberg and Colla, 1997) to construct a 95% confidence interval of the relative probability of plots with cavity trees for stand age class and basal area partitions, respectively, to quantify the significance level of different partitions.

Within each terminal node of the best CART model, the frequency of stands with and without cavity trees was calculated for the five Missouri survey units. We constructed the frequency distribution of plot cavity density by grouping plots into categories with width equal to 10 cavity trees/ha. We described the frequency distribution of number of plots within each cavity density category using a three-parameter Weibull fit by weighted least squares (SAS Institute, 1994). The probability density function (pdf) and cumulative distribution function (cdf) of the three-parameter Weibull distribution for cavity tree density (x) are:

$$f(x) = \frac{a}{b}\left(\frac{x-c}{b}\right)^{a-1}\exp\left[-\left(\frac{x-c}{b}\right)^{a}\right] \quad (c \leq x < \infty) \tag{1}$$

$$F(x) = 1 - \exp\left[-\left(\frac{x-c}{b}\right)^{a}\right] \tag{2}$$

where $a > 0$, $b > 0$, and $-\infty < c < \infty$ are the shape, scale, and location parameters, respectively. To obtain the best fit (maximizing the F value), we used the transformed cavity tree density (x_t) in place of the midpoint values of cavity tree density intervals (x) to fit Eq. (1). Hereby, $x_t = 1, 2, \ldots, 11$ represents the midpoints of intervals = 0.1–10.0, 10.1–20.0, 100.1–110, i.e. 5, 15, ..., 105, respectively ($x_t\,(0) = 0$). The predicted cumulative frequency distribution of cavity trees was generated based on Eq. (2) using the estimated parameters (a, b and c) for Eq. (1) and was used to compare the age class and basal area effect.

3. Results

The frequency distribution of cavity tree abundance within the five survey units had a reverse-J shape, and the frequency of occurrence decreased exponentially with increasing cavity tree density (Fig. 2A). No significant difference in frequency distribution was found among the five survey units ($P > 0.37$). The proportion of plots with cavity trees increased with increasing stand age (Fig. 2B). The odds ratio of plots with cavity trees (P(plots with cavity trees)/P(plots

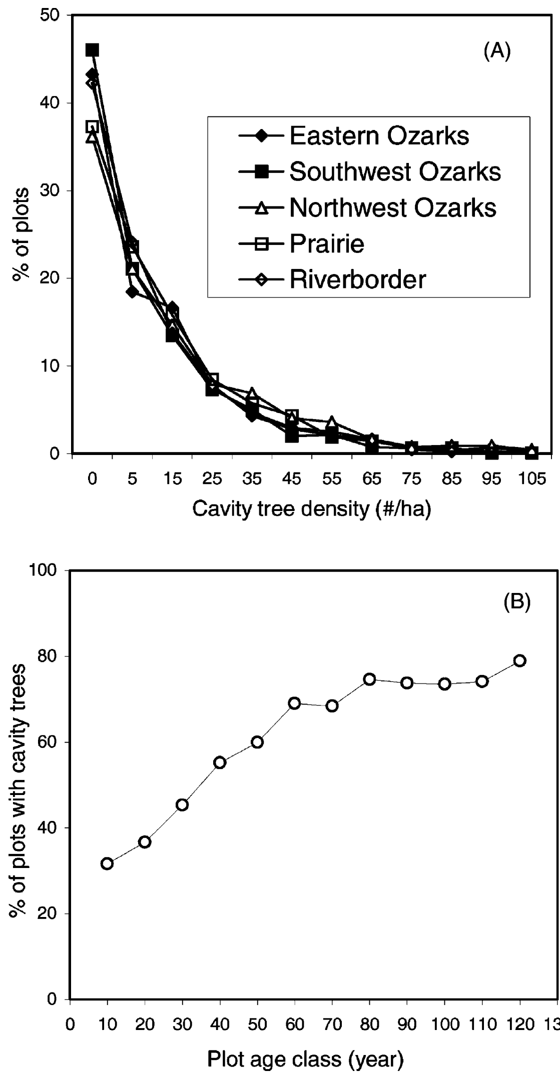

Fig. 2. (A) Frequency distribution of cavity trees by survey unit in Missouri. The frequency distribution of number of cavity trees/ha had a negative exponential form that did not differ significantly ($P > 0.37$) among survey units. (B) Proportion of sample plots (stands) with at least one cavity tree by stand age classes. The probability of a plot having at least one cavity tree increased with increasing stand age.

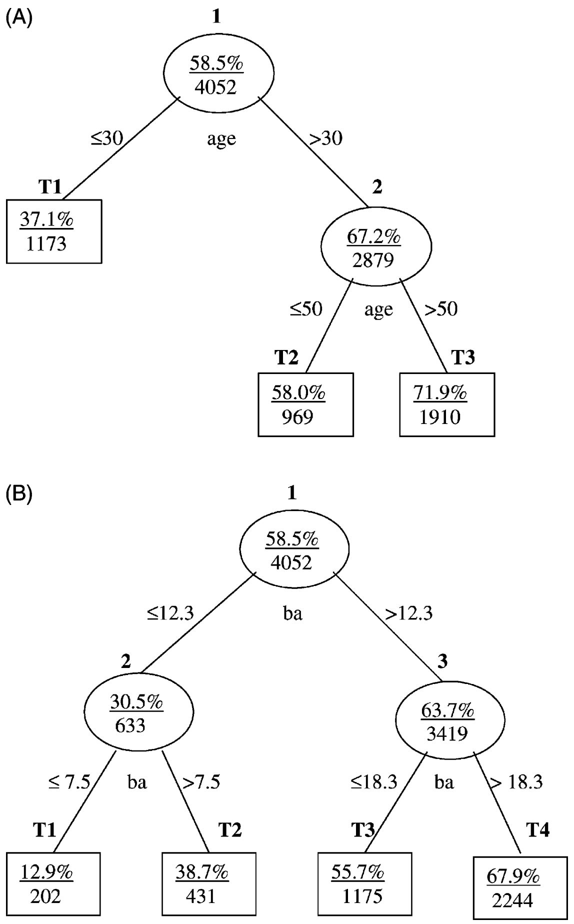

Fig. 3. The classification and regression tree (CART) model of the distribution of plots with cavity trees for the 1989 Missouri Forest Inventory and Analysis (FIA) data: (A) by plot age class; (B) by plot basal area (m^2/ha). Nodes are numbered in bold type. Numerators and denominators are the proportion of plots with at least one cavity tree and the total number of plots within each node, respectively. Lines and their labels indicate classification variables and threshold values for successive nodes.

without cavity trees)) for the entire state was 1.4 (0.585/0.415).

The CART model based on plot age identified three unique groups of plots (represented by terminal nodes T1, T2, and T3, respectively) that differ in their odds ratios (Fig. 3A). The proportion of plots with cavity trees for plots aged ≤30 years), 30–50 years, and >50 years is 37% (odds ratio = 0.59), 58% (odds ratio = 1.38) and 72% (odds ratio = 2.56), respectively. The CART model depicted the main features of

Table 2
The relative probability and 95% confidence interval (CI) of a stand to have cavity trees/snags between age class (year) and basal area (m^2/ha) groups in the CART models (Fig. 3) using five-fold cross validation

Partition	Criterion	Relative probability[a]	95% CI
Age class model (Fig. 3A)			
1	Age > 30 vs. age ≤ 30	1.81	1.57–2.09
2	Age > 50 vs. 30 < age ≤ 50	1.24	1.05–1.46
Basal area model (Fig. 3B)			
1	ba > 12.3 vs. ba ≤ 12.3	2.09	1.74–2.51
2	7.5 < ba < 12.3 vs. ba ≤ 7.5	3.01	1.91–4.75
3	ba > 18.3 vs. 12.3 < ba < 18.3	1.22	1.05–1.41

[a] Probability of a plot with at least one cavity tree occurring in the first group divided by the corresponding probability on the second group. For example, plots with age >30 years are 1.81 times more likely to have cavity trees than plots with age <30 years.

the distribution of plots with and without cavity trees shown in Fig. 2B. Plots without cavity trees are dominant through age 30 years (odds of such a plot having a cavity tree is < 1), while plots with cavity trees are dominant for plots with age greater than 30 years (odds of plots with cavity trees > 1). The probability of a plot > 30 years old having at least one cavity tree is 1.81 times larger than for a plot less than or equal to 30 years old (the 95% five-fold cross validation confidence interval is 1.57–2.09) (Table 2). The CART model further identifies the inflection point of the curves at stand age 50 years (Fig. 2B). The proportion of stands with cavity trees increases dramatically from age 30 to 50 and then increases more gradually after age 50. The probability of a stand greater than 50 years having at least one cavity tree is 1.24 (95% CI: 1.05–1.46) times as large as that of a stand between 30 and 50 years old (Table 2).

Fig. 3B presents a CART model with four terminal nodes (T1, T2, T3 and T4) using plot basal area as the discriminating variable. The proportion of plots with cavity trees for plots with ba ≤ 7.5 m^2/ha (T1), 7.5–12.3 m^2/ha (T2), 12.3 to ≤ 18.3 m^2/ha (T3), and > 18.3 m^2/ha (T4) is 13% (odds ratio = 0.15), 39% (odds ratio = 0.63), 56% (odds ratio = 1.26) and 68% (odds ratio = 2.12), respectively. The five-fold cross validation (Table 2) showed that node pairs differ significantly from each other in the proportion of plots with cavity trees.

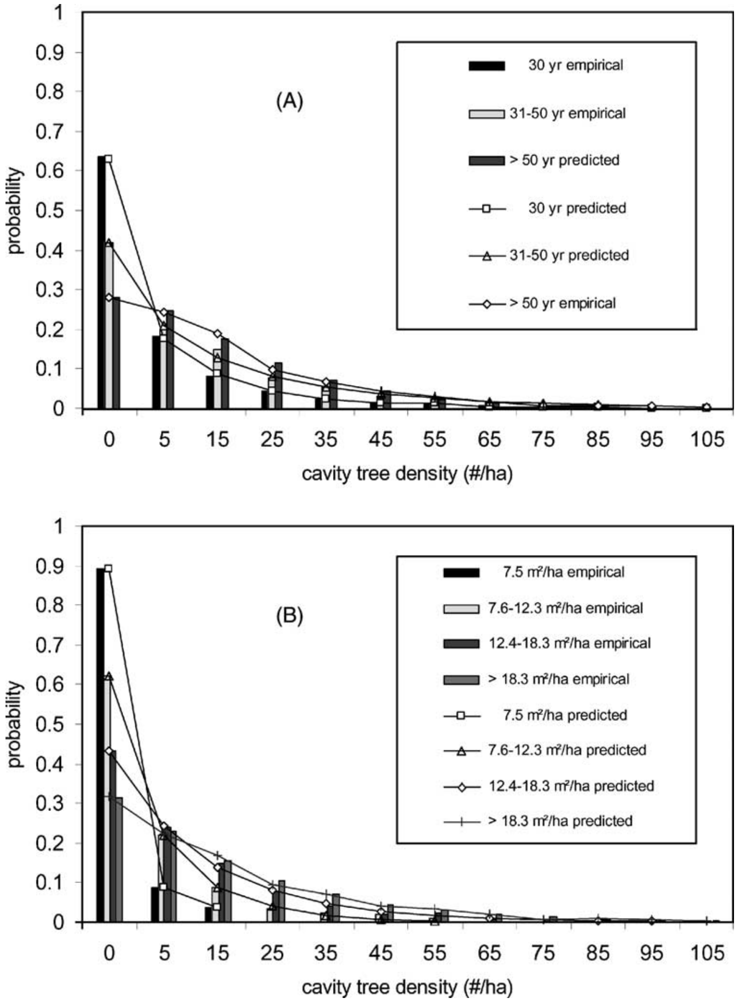

Fig. 4. The empirical (bar) and fitted (line) probability distribution of cavity tree density by Weibull's probability density function (Eq. (1)): (A) by plot age class; (B) by plot basal area (ba, m^2/ha).

Table 3
The fitted parameters and standard errors (in parentheses) of the Weibull probability density function (Eq. (1)) for the terminal nodes in Fig. 3

	Node	a	b	c	F	$P > F$
Age class model (years) (Fig. 3A)						
≤30	T1	0.6768 (0.0515)	0.8912 (0.0776)	−0.3237 (0.0336)	2000	<0.0001
31–50	T2	0.8382 (0.0320)	2.0534 (0.1473)	−0.3849 (0.0494)	1291	<0.0001
>50	T3	1.2851 (0.0619)	2.6110 (0.0568)	−0.6518 (0.1256)	10412	<0.0001
Basal area model (m^2/ha) (Fig. 3B)						
≤7.5	T1	0.3638 (0.4198)	0.1918 (0.1545)	−0.1419 (0.1783)	439	<0.0001
7.6–12.3	T2	0.8877 (0.1166)	0.9920 (0.0776)	−0.4169 (0.0739)	557	<0.0001
12.4–18.3	T3	0.9859 (0.0542)	1.7801 (0.0946)	−0.4671 (0.0705)	766	<0.0001
>18.3	T4	1.0628 (0.0365)	2.5488 (0.0844)	−0.5011 (0.0809)	1206	<0.0001

The frequency distribution of cavity trees within each terminal node of the age class and basal area model (Fig. 4A and B) was well described by the Weibull probability distribution [1]. The F-tests for all fits were significant ($P < 0.0001$) and the parameters have small standard errors (Table 3). The predicted values are very close to the empirical observations (Fig. 4). The proportion of plots with cavities increases with increasing plot age class or basal area for all cavity tree density classes up to 65 cavity trees/ha. Plots containing > 65 cavity trees/ha are rare and comprise approximately 3% of the entire sample. For these sites, factors other than age class or basal area may be influential.

4. Discussion

The large variability and the asymmetric frequency distribution of the number of cavity trees per plot limits the usefulness of the mean cavity tree density (e.g. #/ha) as an indicator on which to base management decisions. General regression analysis on the relationship between cavity density and stand attributes provides little information on the variability among plots in the number of cavity trees/ha. Carey (1983) found mean dbh and site index, the two best predictors, explained only 14% of the variation of cavity tree abundance even though the regression was significant ($P < 0.00001$). He concluded "much of the variability in cavity abundance was random and could not be accounted by topographic position, side index, or stand characteristics (age, dbh, variability in dbh, and tree density). Discrete multivariate analysis of categorical variables (tree species, forest type, dbh class, etc.) was more successful but required a number of tree-specific measurements."

Partitioning stands (or inventory plots) into classes based on age or basal area identifies the broad patterns of cavity tree abundance, but the number of cavity trees per acre is still highly variable within each of those classes (Fig. 4). Therefore, in the context of cavity trees, a distribution-based modeling approach explicitly describing the variation among plots is more informative than a mean-based method (e.g. regression). Fan et al. (2002) explored the distribution of cavity trees by tree-specific measurements (e.g. dbh, decay class, species group) using the non-parametric CART model and identified categories which differ significantly in cavity tree distribution. For this application, the classification and regression tree model was used to search for the distribution patterns of plots with and without cavity trees by age class and basal area. The hierarchical structure of CART provides an intuitive way to view the intrinsic structure of the distribution of plots with (or without) cavity trees by plot age class and basal area and the significance of the predictor variables and interactions. In this study, the probability distribution pattern of plots with (or without) cavity trees by age class and basal area was delineated by CART, respectively, as three and four disjoint regions (terminal nodes in Fig. 3), which differ significantly in the probability that plots will have cavity trees/snags.

The CART and Weibull probability distribution function (Fig. 4), in combination, present a clearer picture of the distribution of cavity trees among plots with different age class and basal area. The cumulative Weibull distribution function (cdf) showing the cumulative frequency of plots by cavity tree density classes (Fig. 5) is of particular utility to managers because it allows them to easily see the probability of achieving a specified minimum number of cavity trees for plots of a particular age class or basal area level. For example, if the desired number of cavity trees is at least five per hectares then based on Fig. 5A the probability of having fewer than five cavity trees/ha is 0.81 for stands < 30 years old, 0.62 for stands 31–50 years old, and 0.52 for stands greater than 50 years old. The corresponding success probability of five or more cavity trees/ha is estimated as 1−the probability of fewer than five cavity trees (i.e. 0.19 for stands < 30 years old, 0.38 for stands 31–50 years old, and 0.48 for stands greater than 50 years old). The same result can be obtained analytically rather than graphically by substituting the coefficients from Table 3 into Eq. (2), solving for a given cavity tree density (x), and subtracting that probability from 1. This approach is easily implemented using a spreadsheet or computer program.

In this study, plot age class and basal area were chosen as the predictor variables based on the intensive exploratory data analysis. They are the two most significant single variables at the stand (plot) level affecting cavity tree distribution, but their additive effect on cavity tree distribution is partial. This result

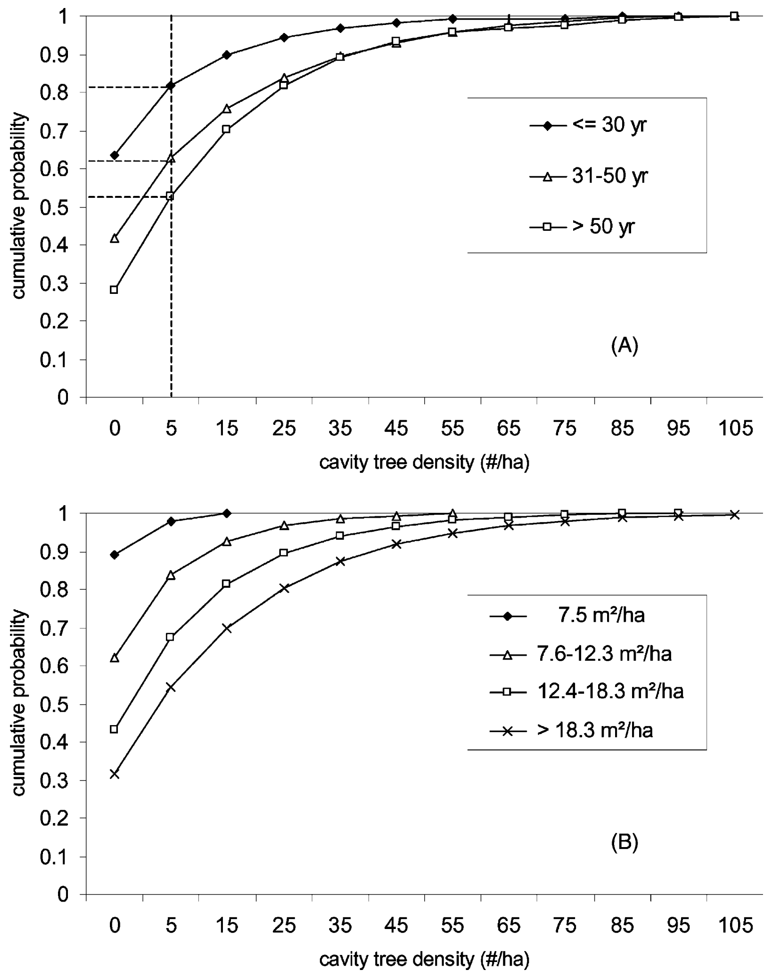

Fig. 5. The fitted cumulative probability distribution of cavity tree density by Weibull's cumulative distribution function (Eq. (2)): (A) by plot age class; (B) by plot basal area. This result can be used to readily estimate the expected proportion of plots that will have a specified minimum number of cavities/ha. The dashed lines in panel A indicate the probability that stands in each age group will have fewer than five cavity trees/ha.

is consistent with previous studies (e.g. Carey, 1983; Allen and Corn, 1990; Fan et al., 2002). Actually, stand age class and basal area are highly correlated and basal area is a function of stand age, density and site index. Age and basal area describe the same accumulation process of cavity trees as stand develops from two different perspectives. Other stand variables such as forest type, slope, aspect, and site index were tested but were not significant in the best CART model, indicating that their effect on the distribution of plots with and without cavity trees was negligible.

Interestingly, the three age class groups identified by the CART model (Fig. 3A) matched the three stand size classes typically used by forest managers to describe stand size structure: seedling/sapling, poletimber, and sawtimber. Consequently, age or size class can be used interchangeably to evaluate cavity tree abundance in a forested landscape. For instance, among the three distinct age (size) groups identified by CART, seedling/sapling stands (stands $\leq$ 30 years old) contribute little to cavity tree abundance, because over 60% of these stands have no cavity trees (Figs. 3–5). Poletimber stands (stands with age > 30 years and $\leq$ 50 years) have a moderate number of cavity trees/ha; sawtimber stands (stands > 50 years old) are the major reservoir of cavity trees. However, sawtimber stands are also commonly a target of timber harvesting activities. To achieve multiple management goals, forest managers and planners need to integrate cavity tree distributions and dynamics into their management plans.

The structure of CART or the number of terminal nodes reflected the major pattern inherent in the data and varied significantly with the structure (such as plot age structure) or some influential points in the data. The cross-validation confidence intervals provide a measure for both model selection and evaluation of the strength of each partition in the CART. Each partition in the CART models presented in Fig. 3 is significant (e.g. the 95% confidence intervals for the relative probability in Table 2 do not include 1). In the age class CART model (Fig. 3A), no further partition was implemented with plots >50 years. However, Fan et al. (2002) reported that cavity tree abundance in old-growth forests (> 150 years old) is double then that in the second-growth forests > 110 years. We believe that the age structure of plots > 50 years (Table 1) explained this discrepancy. Among plots > 50 years, age classes 50–110 are dominant and fewer than 3% of plots are older than 110 years. The proportion of plots with cavity trees among plots between 50 and 110 years reaches a plateau (Fig. 2B). A significant partition for plots > 110 years old should be possible if a sufficient number of older plots were available in the data used for analysis.

The reverse-J shape distribution pattern of cavity trees within each age and basal area group (Fig. 4) is a reflection of a series of factors and processes that lead to cavity formation. And the pattern should hold for projected future forest conditions if the cavity formation processes are not greatly altered. Given the highly stochastic characteristics of cavity tree distribution by stands and by individual trees (e.g. Carey, 1983; Allen and Corn, 1990; Fan et al., 2002), the primary utility of the fitted models presented here is to predict total cavity tree abundance for many stands across a landscape or large region and to evaluate the potential impact of timber management or other disturbances on the future cavity tree resource, rather than to predict cavity tree availability for individual stands. An obvious conclusion drawn from the fitted cavity tree distribution models, for instance, is that intensive timber management that increases the acreage of juvenile forests or decreases stand basal area will inevitably decrease the cavity tree resource (Conner et al., 1975; Cline et al., 1980; McComb and Noble, 1980; Mannan and Meslow, 1984; Zarnowitz and Manuwal, 1985; Wilson, 1996). The allocation of seedling/sapling, poletimber, and sawtimber stands on a landscape needed to maintain a specified number of cavity trees/snags can be readily estimated based on the fitted probability distribution models (Table 3 and Figs. 4 and 5). In many respects, the models estimating cavity abundance by age class are analogous to yield tables that estimate timber volume by age class and have long been used to guide timber management decisions. For example, an upland oak forest managed on an even-aged, 100-year rotation would have 30% of the area in the seedling/sapling size class (< 30 years old), 20% in the pole size class (31–50 years old) and the remaining 50% in the sawlog size class (> 50 years old). Based this age distribution, on Fig. 5, and on the previous example, the proportion of the total forest area that will have fewer than five cavity trees per acre is 61%; the remaining 39% of the area will have five or more cavity trees per acre. Lengthening the rotation age would increase the proportion of the forest area in older age classes and increase the total proportion of the forest with a specified minimum number of a cavity trees. Moreover, Fig. 4 indicates the range of variation among sites in the total number of cavity trees/ha. As shown in Fig. 4A, the majority of sites will have five or fewer cavity trees/ha, but a few sites will have more than 75 cavity tree/ha.

An interesting extension and application of the results of this study would be to link the fitted probability models to a landscape-change model such as LANDIS (He and Mladenoff, 1999) to simulate cavity abundance through time across a forest landscape under differing disturbance scenarios (e.g. Gustafson et al., 2000; Shifley et al., 2000). By linking the probability distribution models of cavity tree density by age groups to the projected stand age classes across a landscape, the dynamics of cavity tree abundance on a specified landscape under a variety of timber management scenarios and natural disturbance regimes can be simulated directly. Likewise, the probability distribution models of cavity tree density by basal area groups can be incorporated readily into Forest Inventory and Analysis data to analyze the dynamics of cavity tree abundance over different sampling periods. This information can help formulate broad-scale management guidelines for wildlife habitat and aid in understanding the large-scale, long-term consequences of proposed management activities.

The stand-scale cavity estimation models presented in this paper fit into a management information hierarchy. The models presented here are efficient and appropriate for landscape-scale evaluations of management practices on the cavity resource over space and through time (i.e. across thousand or hundreds of thousands of hectares in conjunction with landscape forest simulation models). Their application requires information only on stand age class or basal area. However, these cavity models are not well suited for estimation of cavity abundance within individual stands. Other cavity models that utilize stand-level inventory information on species, tree size, and/or decay class are available for that purpose (e.g. Allen and Corn, 1990; Fan et al., 2002). These models improve site-level estimation of cavity resources, but their application requires tree-level detail that is rarely available across a large landscape. At yet a finer level of detail, management prescriptions for individual stands are best prepared with an explicit field inventory of the current cavity abundance (by cavity size and location) and an understanding of the cavity requirements of each desired wildlife species. Species or individual tree level information on cavity and snag distribution (Fan et al., 2002) guides managers in the retention of cavity trees or trees that are likely to become cavity trees. With such a hierarchical approach, the site level management prescriptions have the benefit of a larger landscape context, both currently and as that landscape might exist in the future. Data requirements for analysis increase with increasing resolution from landscapes to stands to trees within stands. By considering the interaction between local habitat factors, landscapes, and regional contexts, multi-scale management planning for cavity trees can contribute to regional-scale resource assessments and identification of conservation priorities and goals as part of hierarchical approach that integrates many other aspects conservation planning (Thompson and DeGraaf, 2001).

The assumption in our presentation of this methodology is that all cavity trees are equally valuable and that a simple count of cavity trees is sufficient to quantify the cavity resource for many purposes. No distinction has made by cavity size or cavity location on a tree, although such criteria may be important in evaluating habitat quality for certain wildlife species. Provided field data are available for calibration, the general methodology is amenable to a much more detailed classification of cavity types. The limiting factor in such endeavors is typically the availability of a sufficiently large and detailed cavity inventory.

5. Conclusion

1. In Missouri, cavity tree abundance varied widely among plots. The cavity tree density ranged from 0 to 110 trees/ha, but the proportion of plots decreased dramatically in a reverse-J manner with the increase of cavity tree density. The overall odds ratio of plots with cavity trees was 1.4 (0.585/0.415) for the entire state. No significant difference in cavity tree distribution was found among the five survey units.
2. Plot age class and basal area were the top two indicators with which the distribution of cavity tree density changed significantly. The proportion of plots with at least one cavity tree/ha was 37, 58 and 72% within plots = 30 years (seedling/sapling), 31–50 years (poletimber), and > 50 years (sawtimber), respectively. Sawtimber stands are the major reservoir of cavity trees, and seedling/sapling plots contribute little to the cavity tree resource. Therefore, management of cavity trees, as required by many wildlife conservation issues, must consider the allocation of stands with different ages.
3. Plot basal area and age were strongly correlated. However, basal area is usually easier to measure than stand age and thus is often more useful in stand management. The relationship of plot basal area to cavity tree abundance was seen from the fact that the proportion of plots with at least one cavity tree/ha increased from 13 to 68% with a change in basal area from ≤ 7.5 to > 18.3 m^2/ha.
4. The distribution of cavity tree density within each of the disjoint plot clusters identified by CART using plot age class and basal area as the predictors was well described by the Weibull probability density function. As the plot age class

or basal area class increased across these plot clusters, the proportion of plots without cavity trees decreased, the proportion of plots with 1–65 trees/ha increased, and the distribution of cavity tree density became less skewed. Plots > 65 cavity trees/ha were less than 3% in percentage and may be the consequence of random factors not captured sufficiently by plot age class or basal area.

5. CART and the Weibull function, in combination, provide a useful tool for managers and planners to evaluate and analyze regional cavity tree resource and timber management effect quantitatively and probabilistically. They can also be linked with landscape level models such as LANDIS to simulate cavity tree dynamics under different management scenarios.

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References

Allen, A.W., Corn, J.G., 1990. Relationships between live tree diameter and cavity abundance in a Missouri oak-hickory forest. North J. Appl. For. 7, 179–183.

Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1984. Classification and Regression Trees. Wadsworth and Brooks, Monterey, CA, USA.

Carey, A.B., 1983. Cavities in Trees in Hardwood Forests. USDA For. Serv. Gen. Tech. Rep. RM-99. Snag Habitat Management Symposium, p. 167–184.

Cline, S.P., Berg, A.B., Wight, H.M., 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44 (4), 773–786.

Conner, R.N., Hooper, R.G., Crawford, S.H., Mosby, H.S., 1975. Woodpecker nesting habitat in cut and uncut woodlands in Virginia. J. Wildl. Manage. 39, 144–150.

Degraaf, R.M., Shigo A.L., 1985. Managing Cavity Trees for Wildlife in the Northeast. USDA For. Serv. Gen. Tech. Rep. NE-101.

Fan, Z., Shifley, S.R., Spetich M.A., Thompson, F.R., Jr., Larsen, D.R., 2002. Distribution of cavity trees in midwestern old-growth and second-growth forests. Can. J. For. Res. (in review).

Franklin, J.F., Shugart, H.M., Harmon, M.E., 1987. Tree death as an ecological process. Bioscience 37, 550–556.

Gustafson, E.J., Shifley, S.R., Mladenoff, D.J., Nimerfro, K.K., He, H.S., 2000. Spatial simulation of forest succession and timber harvesting using LANDIS. Can. J. For. Res. 30, 32–43.

Hahn, J.T., Spencer, J.S., 1991. Timber Resource of Missouri, Statistical Report, 1989: An Analysis. Resource Bulletin NC-119. USDA, Forest Service, North Central Forest Experiment Station, St. Paul, MN. p. 123.

Hansen, H.L., 1966. Silvical characteristics of tree species and decay process as related to cavity production. In: Proceedings of the Wood duck Management and Research: A Symposium. Wildlife Management Institute, Washington, DC. pp. 65–69.

He, H.S., Mladenoff, D.J., 1999. An object-oriented forest landscape model and its representation of tree species. Ecol. Model. 119, 1–19.

Healy, W.M., Brooks, R.T., DeGraaf, R.M., 1989. Cavity trees in sawtimber-size oak stands in central Massachusetts. North J. Appl. For. 6, 61–65.

Jensen, R.G., Kabrick, J.M., Zenner, E.K., 2002. Tree cavity estimation and verification in the Missouri Ozarks. In: Shifley, S.R., Kabrick, J.M. (Eds.), Proceedings of the Second Missouri Ozark Forest Ecosystem Project Symposium: Post-Treatment Results of the Landscape Experiment. USDA For. Serv. Gen. Tech. Rep. NC-227.

Kowal, D.M., Husband, T.P., 1996. Characteristics of trees with excavated cavities used by birds in Rhode Island. North J. Appl. For. 13 (1), 16–18.

Mannan, R.W., Meslow, E.C., 1984. Bird populations and vegetation characteristics in managed and old-growth forests, northeastern Oregon. J. Wildl. Manage. 48, 1219–1238.

Mannan, R.W., Meslow, E.C., Wight, H.M., 1980. Use of snags by birds in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44 (4), 787–797.

McClelland, B.R., Frissell, S.S., 1975. Identifying forest snags useful for hole-nesting birds. J. For. 73, 414–417.

McClelland, B.R., McClelland, P.T., 1999. Pileated woodpecker nest and roost trees in Montana: links with old-growth and forest "health". Wildl. Soc. Bull. 27 (3), 846–857.

McClelland, B.R., Frissell, S.S., Fischer, W.C., Halvorson, C.H., 1979. Habitat management for hole-nesting birds in forests of western larch and Douglas fir. J. For. 77, 480–483.

McComb, W.C., Noble, R.E., 1980. Effects of single tree selection cutting upon snag and natural cavity characteristics in Connecticut. Trans. Northeast. Sect., The Wildl. Soc., Fish and Wildl. Conf. 37, 50–57.

McComb, W.S., Bonney, S.A., Sheffield, R.M., Cost, N.D., 1986. Den tree characteristics and abundance in Florida and south Carolina. J. Wildl. Manage. 50, 584–591.

Miles, P.D., Brand, G.J., Alerich, C.L., Bednar, L.F., Woudenberg, S.W., Glover, J.F., Ezell, E.N., 2001. The Forest Inventory and Analysis Database Description, Users Manual Version 1.0. USDA For. Serv. Gen. Tech. Rep. NC-218, p. 130.

North Central Forest Experiment Station. 1986. North Central Region Forest Inventory and Analysis Field Instructions, Missouri. USDA For. Serv., North Central Forest Experiment Station, St. Paul, MN. p. 115.

SAS Institute. 1994. SAS/STAT User's Guide. Version 6. Fourth ed. SAS Institute, Cary, NC, USA.

Scott, V.E., Whelan, J.A., Svobond, P.L., 1980. Cavity nestng birds and forest management. In: DeGraaf, R.M. (Ed.), Proceedings of the Workshop on Management of North Central and Northeastern Forests for Non-game Birds. USDA For. Serv. Gen. Tech. Rep. NC-51, pp. 311–324.

Sedgwick, J.A., Knopf, F.L., 1986. Cavity-nesting birds and the cavity-tree resource in plains cottonwood bottomlands. J. Wildl. Manage. 50 (2), 247–252.

Shifley, S.R., Thompson Jr., F.R., Larsen, D.R., Dijak, W.D., 2000. Modeling forest landscape change in the Missouri Ozarks under alternative management practices. Comput. Electron. Agric. 27, 7–24.

Spencer, J.S., Jr., Roussopoulos, S.M., Massengale, R.M., 1992. Missouri's Forest Resource, 1989: An Analysis. Resource Bulletin NC-139. USDA, Forest Service, North Central Forest Experiment Station, St. Paul, MN, 84 p.

Spetich, M.A., 1995. Characteristics and Spatial Pattern of Old-Growth Forests in the Midwest. Ph.D. Dissertation, Purdue University, West Lafayette, IN, 276 p.

Steinberg, D., Colla, P., 1997. CART—Classification and Regression Trees. Salford Systems, San Diego, CA.

Thompson, F.R., DeGraaf, R.M., 2001. Conservation approaches for woody, early successional communities in the eastern United States. Wildl. Soc. Bull. 29 (2), 483–494.

Titus, R., 1983. Management of snags and cavity trees in Missouri: a process. In: Proceedings of the Snag Habitat Management Symposium. USDA For. Serv. Gen. Tech. Rep. RM-99, p. 51–59.

Van Balen, J.H., Booy, C.J.H., Franeker, J.A., Osieck, E.R., 1982. Studies on hole-nesting birds in natural nest site 1: availability and occupation of natural nest sites. Ardea 70, 1–24.

Wilson, J.D., 1996. Missouri Breeding Bird Changes: 1967–1995. Missouri's Forest, Fish, and Wildlife Conference, Osage Beach, MO.

Zarnowitz, J.E., Manuwal, D.A., 1985. The effects of forest management on cavity-nesting birds in northwestern Washington. J. Wildl. Manage. 49 (1), 255–263.