Abundance and Size Distribution of Cavity Trees in Second-Growth and Old-Growth Central Hardwood Forests

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ABSTRACT: *In central hardwood forests, mean cavity-tree abundance increases with increasing stand-size class (seedling/sapling, pole, sawtimber, old-growth). However, within a size class, the number of cavity trees is highly variable among 0.1-ha inventory plots. Plots in young stands are most likely to have no cavity trees, but some plots may have more than 50 cavity trees/ha. Plots in old-growth stands often had 25 to 55 cavity trees/ha, but individual plots ranged from 0 to 155/ha. The Weibull probability density function was used to mathematically describe the variation in cavity-tree abundance for plots in stands of differing size (or age) class. A graph of the cumulative probability of cavity-tree abundance is a particularly easy way for managers to estimate the probability that a stand of a given size class will have any specified number of cavity trees per hectare. Results for individual plots or stands can be combined to estimate cavity abundance probabilities for landscapes. Because the results are presented in terms of plot-size classes (or age classes), this approach to cavity tree estimation is compatible with relatively simple forest inventory systems. North. J. Appl. For. 22(3):162–169.*

Key Words: Snags, Indiana, Illinois, Missouri, wildlife habitat.

Contemporary forest ecosystem management requires managers to consider wildlife habitat quality in their management plans. Snags (standing dead trees), cavity trees (either live or dead trees with cavities suitable as wildlife habitat), and down dead logs are important habitat for a variety of wildlife species (Carey 1983, Robb et al. 1996, Betts 1998, Loeb 1999, Yetter et al. 1999, White et al. 2001, Bowman et al. 2000). These same components of the forest also can harbor tree-destroying insects or diseases or contribute to fire risk. Thus, multiple-use forest management requires balancing the benefits and risks associated with snags, cavity trees, and down dead wood. In forests intensively managed for timber, the number of snags, cavity trees, and down dead logs usually is reduced through short harvest rotations and intermediate silvicultural treatments that remove cull, dead, or dying trees. The reduction of these "habitat" trees in managed forests has the potential to negatively impact the quality of wildlife habitat and carrying capacity. Thus, sustainable resource management must explicitly address the compatibility of management practices with ecosystem functions and balance the tradeoffs between different management goals such as timber production and wildlife habitat protection (Diaz and Bell 1997, Gustafson and Diaz 2002, Gutzwiller 2002, Loehle et al. 2002).

The quantity and distribution of live trees, snags, and down dead logs have been well addressed in certain tree and stand level models (e.g., Spetich et al. 1999 or the Forest Vegetation Simulator (FVS); Crookston and Havis 2002, Teck et al. 1997), but comparatively little effort has been directed at modeling cavity-tree abundance and dynamics. This is due in large part to the difficulty (1) in detection and

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inventory of the cavity resource (Jensen et al. 2002); and (2) in predicting cavity-tree abundance based on tree or stand attributes.

Stand age or stand-size class, both for individual stands and for stands arranged on a landscape, are important factors in forest management and planning. Central Hardwood forest stands often are categorized into three broad size classes based on stand age or stage of development: seedling/sapling (1–30 years), pole (31–50 years), and sawtimber (>50 years), which differ significantly in structure and function and which typically require different management practices and silvicultural treatments. Stand age and/or size classes also are important indicators of cavity-tree abundance in the Central Hardwood region (e.g., Carey 1983, Healy et al. 1989, Allen and Corn 1990, Fan et al. 2003a). The objectives of this study were to quantify the frequency and size distribution of cavity trees in seedling/sapling, pole, sawtimber, and old-growth stands based on plot data. The information can be directly used in forest-level planning to estimate current cavity-tree abundance and change in cavity-tree abundance over time. Because cavity-tree abundance is highly variable among stands, the procedures used in this study explicitly account for that variability and use it as part of the estimation process.

Methods

Data

Data on the density distribution of cavity trees among second-growth seedling/sapling, pole, and sawtimber stands came from the 1989 inventory of Missouri forests conducted by the Forest Inventory and Analysis unit of the North Central Forest Experiment Station, USDA Forest Service (Hahn and Spencer 1991, Spencer et al. 1992, Miles et al. 2001). The 1989 Missouri forest inventory was a systematic sample of all timberland in the state. The sample is comprised almost exclusively of second-growth forests and encompasses a wide range of forest conditions that is perhaps best described as a woods-run average with regard to past disturbance by fire, weather, harvest, and other agents. There was virtually no information about how past management practices may have directly altered the cavity resource on individual plots (e.g., through cavity-tree retention), but the presumption is that the majority of past timber harvesting that occurred previously on sampled plots was a combination of diameter-limit cutting or high grading on plots in the sawtimber size class. Such practices often leave behind cavity trees as culls.

Each inventory plot was comprised of 10 subplots spread over approximately 0.4 ha. Trees ≥13 cm dbh were sampled with an 8.6-factor angle gauge (m^2/h) on each subplot, and subplots were combined to obtain estimates for the entire plot. Species, diameter, size of the largest visible cavity (smallest dimension to the nearest inch), and other characteristics were recorded for each sampled tree. The inventory included more than 141,000 trees sampled on 4,052 inventory plots (Table 1). For each 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 considered nonstocked and excluded from analysis. The cavity-tree density for each plot was expanded to a per hectare estimate for analysis.

Data on the number and variability of cavity trees among old-growth forests came from an inventory of remnant old-growth tracts in Indiana, Illinois, and Missouri (Spetich 1995, Shifley et al. 1995, 1997, Spetich et al. 1999). From 1992 to 1994, 15 remnant old-growth tracts in Missouri, Illinois, and Indiana were inventoried for cavities in association with a general inventory of forest composition and structure (Table 1). Trees ≥10 cm dbh were inventoried on 0.1-ha circular plots. Species, diameter, status (live or dead), and other characteristics were recorded for each tree. Cavities were observed from the ground, and natural and excavated openings at least 2 cm in size (smallest dimension) were recorded. Trees were considered "cavity trees" if they had at least one visible cavity, regardless of the cavity size or location. Tree-crown class (dominant, co-dominant, intermediate, overtopped) and crown ratio (by 10% classes) also were recorded for each tree. Decay classes based on a classification scheme described by Maser et al. (1979) were recorded for live trees (healthy, declining in vigor) and dead trees (recently dead with tight bark, dead with loose bark, bole free of bark or nearly so, broken top and clean of bark, broken top and largely decomposed). Slope percent, slope position, and aspect were recorded for each plot. The number of inventory plots varied from four to 30 per tract with a total of 294 plots with more than 8,000 measured trees (Table 1). Cavity-tree density per plot was expanded to a per hectare value for analysis. More information on tract locations, inventory procedures, and vegetation characteristics can be found in Spetich (1995), Spetich et al.(1999), and Shifley et al. (1995, 1997).

Statistical Analysis

Cavity-tree density (number/ha), as a measure of cavity-tree abundance in a plot, theoretically can be any number between zero and the total number of trees per hectare. For a large sample of plots within a given stand-size class (e.g., for pole-size stands), a range of cavity-tree densities is typically observed and can be used to graph a frequency distribution of the number of cavity trees per hectare for that size class. For young plots, the cavity-tree frequency distribution tends to be reverse-J shaped (negative exponential), with most plots having no cavity trees or only a few cavity trees per hectare (Fan et al. 2003b). Older plots (e.g., sawlog size class or old-growth) typically have more cavities, and the frequency distribution of the number of cavities per hectare shifts toward a bell-shape (unimodal). For consistency and simplicity, the Weibull distribution (Bailey and Dell 1973) was applied to quantify the frequency distribution of cavity-tree density in seedling/sapling, pole, sawtimber, and old-growth plots. The probability (frequency) density function (pdf) of the three-parameter Weibull distribution for cavity-tree density is:

Table 1. Location, sample size, and overstory characteristics for sampled sites. Includes trees ≥13 cm dbh for Missouri FIA sample and trees ≥10 cm for old-growth sites.

Site name	State	No. plots	Live cavity trees	Dead cavity trees	Total cavity trees	All live trees	All dead trees	Dominant tree species
			. . . .(trees/ha)	. . . .				
State inventory								
Missouri FIA	MO	4,052	10	1	11	332	22	White oak (*Q. alba L.*); black oak (*Q. velutina Lam.*); post oak (*Q. stellata Wangenh.*)
Old growth sites								
Funks Grove	IL	4	45	8	53	273	28	Sugar maple (*Acer saccharum L.*); bur oak (*Quercus macrocarpa Mich.*); green ash (*F. pennsylvanica Marsh.*)
Starved Rock	IL	4	40	10	50	340	33	N. red oak (*Q. rubra L.*); white oak; black oak
Spitler Woods	IL	30	49	8	57	406	39	White oak; sugar maple; n. red oak
Bendix Woods	IN	4	33	0	33	283	15	American beech (*Fagus grandifolia Ehrh.*); sugar maple; red elm (*Ulmus rubra Muhl.*)
Calvert-Porter Woods	IN	4	10	5	15	270	25	Sugar maple; sycamore (*Platanus occidentalis L.*); yellow-poplar (*Liriodendron tulipifera L.*)
Davis-Purdue	IN	30	47	11	58	308	30	White oak; n. red oak; sugar maple
Donaldson's Woods	IN	30	59	9	68	239	16	White oak; yellow-poplar; American beech
Hemmer Woods	IN	30	32	4	36	258	23	White oak; black oak; n. red oak
Hoot Woods	IN	4	45	3	48	243	8	American beech; white oak; sugar maple
Laughery Bluff	IN	30	15	7	22	216	24	Yellow-poplar; sugar maple; American beech
Lubbee Woods	IN	4	33	3	36	248	10	American beech; white oak; sugar maple
Pioneer Mothers	IN	30	54	12	66	260	17	Sugar maple; American beech; white oak
Big Spring	MO	30	36	11	47	467	39	White oak; black oak; scarlet oak (*Q. coccinea Muenchh.*)
Dark Hollow	MO	30	52	12	64	331	36	N. red oak; white oak; American basswood (*Tilia americana L.*)
Engelmann Woods	MO	15	72	5	77	398	31	Sugar maple; red oak; chinkapin oak (*Q. muehlenbergii Engelm.*)
Roaring River	MO	15	57	7	64	442	41	White oak; black oak; n. red oak

$$f(x_t) = \frac{a}{b}\left(\frac{x_t - c}{b}\right)^{a-1} \exp\left[-\left(\frac{x_t - c}{b}\right)^{a}\right] \quad (x_t = 0, 1, 2, \ldots)$$

where $a > 0$, $b > 0$, and $c < x_t$ are the shape, scale, and location parameters, respectively, and $f(x_t)$ is the probability of transformed cavity-tree density x_t. For analysis, cavity-tree density was first categorized into a set of intervals of 10 cavity trees/ha (e.g., 0, 0.1–10, 10.1–20, . . .) because the 0.1-ha plots used to sample the old-growth sites measured values in units of 10 trees/ha. Thus, $x_t = 1, 2, \ldots$ represents the intervals = 0.1–10.0, 10.1–20.0, . . . , respectively; $x_t = 0$ represents cavity-tree density 0. The transformed cavity-tree density (x_t) was used in place of the midpoint values of cavity-tree density intervals to fit the Weibull function so that the frequency distribution of the cavity-tree number per plot and the associated per hectare values conformed to one another. The Gauss-Newton iterative method of NLIN procedure (SAS Institute Inc. 2000) was used to estimate the parameters of the Weibull function with the estimated initial values of a, b, and c as 10, 8 and −0.2, and 0.5, 2, and −0.3 for the old-growth and second-growth forests, respectively.

Cavity trees and snags within each plot of the second-growth and old-growth forests then were classified into three size groups, small (dbh ≤ 25 cm), medium (25 cm < dbh ≤ 48 cm), and large (dbh > 48 cm), to reflect potential use by different wildlife species (Titus 1983). The percentages of the small, medium, and large cavity trees were calculated, and the approximate 95% confidence intervals were generated using the resampling (bootstrap) method (Efron 1979, Efron and Tibshirani 1993) for seedling/sapling, pole, sawtimber, and old-growth stands, respectively.

Results

Second-growth FIA data in Missouri and combined old-growth data from Missouri, Illinois and Indiana showed substantial variability among plots in the number of cavity trees. Calculated cavity-tree density (number/ha) ranged from 0 to 155. The frequency distribution of cavity trees varied among second-growth plots representing different age or size classes and between second-growth and old-growth plot (Figure 1). The frequency distribution shifted from a reverse-J shape (negative exponential) shape in second-growth sample to a bell shape (or unimodal) distribution for old-growth sample (Figure 1). These frequency distributions were well described by the three-parameter Weibull function using the transformed cavity-tree density as the predictor; no evidence of detectable residual patterns was found with the fitted model. The observed and fitted probabilities (frequencies) for different cavity-tree density classes are very close (Table 2 and Figure 1).

In second-growth forests, plots with 0–15 cavity trees/ha comprise 91, 75, and 70% of the total plots in the seedling/sapling, pole, and sawtimber stands, respectively (Figures 1 and 2). Moreover, as shown by Figure 1, plots with zero cavity trees are the most dominant individual class, accounting for 66, 43, and 29% of the total plots in the

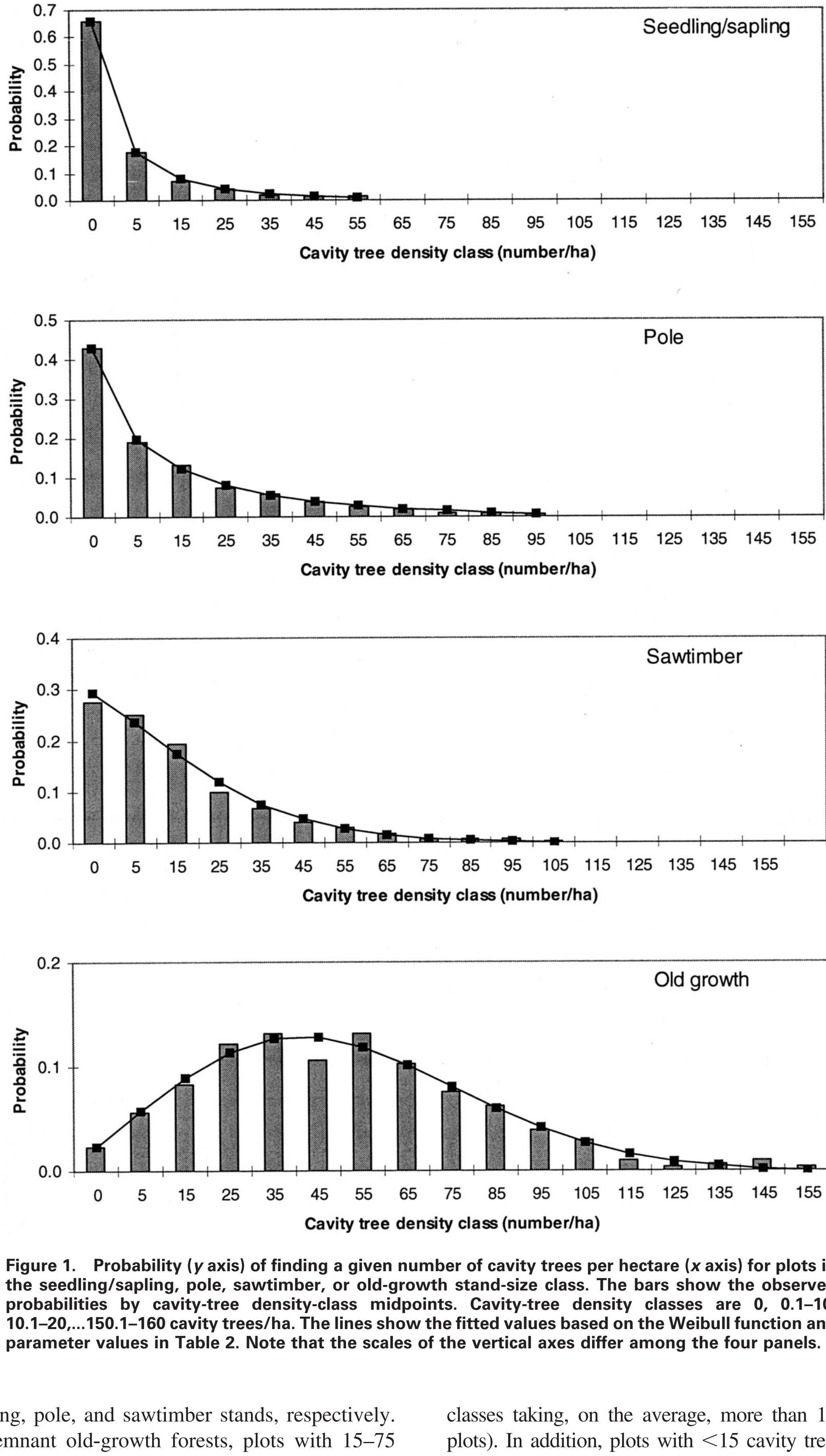

Figure 1. Probability (*y* axis) of finding a given number of cavity trees per hectare (*x* axis) for plots in the seedling/sapling, pole, sawtimber, or old-growth stand-size class. The bars show the observed probabilities by cavity-tree density-class midpoints. Cavity-tree density classes are 0, 0.1–10, 10.1–20,...150.1–160 cavity trees/ha. The lines show the fitted values based on the Weibull function and parameter values in Table 2. Note that the scales of the vertical axes differ among the four panels.

seedling/sapling, pole, and sawtimber stands, respectively. Within the remnant old-growth forests, plots with 15–75 cavity trees/ ha comprised 76% of the total plots (individual classes taking, on the average, more than 10% of the total plots). In addition, plots with <15 cavity trees/ha comprised only 8% of the total plots within old-growth forests (Figure 1).

Discussion

The utility of cavity trees to cavity-dependent wildlife varies with tree size (or more accurately, cavity size). In the old-growth forests, cavity trees were distributed evenly across the three size groups; the proportion of the small (13–25 cm), medium (26–48 cm), and large (>48 cm) cavity trees fluctuated around 37, 34, and 29%, respectively, with a range less than ±3% at the 95% confidence level. However, in the second-growth forests, large cavity trees are relatively scarce (≤10%), and small and medium-sized cavity trees constitute the majority (>90%) of the cavity tree reservoir (Table 3). Plots in sawtimber stands had more medium and large cavity trees than those in seedling/sapling and pole stands, although the magnitude of the difference between them ranged from 2 to 3% for large cavity trees (Table 3). The difference in the proportion of medium-sized cavity trees between sawtimber stands and seedling/sapling/pole stands was more than 10%. The seedling/sapling stands and the pole stands were similar in their proportion of the three cavity tree size groups (Table 3).

Stand-size class (or stand age) is a strong indicator of patterns of cavity-tree abundance at a large scale, but the number of cavity trees on a 1-ha plot is a random variable, and there is substantial variation among plots within a given stand-size class (Figure 1). Attempts to link a stand's mean cavity-tree abundance with variables such as stand age or site index (as is commonly done with timber volume or yield) have been of limited utility due to the enormous variability in cavity-tree abundance (Carey 1983). As demonstrated by Fan et al. (2003b) and this study (Figure 1), cavity-tree densities follow an asymmetric frequency (i.e., probability) distribution. Under these circumstances, simple descriptive statistics such as mean and variance of cavity trees do not adequately capture the variation in cavity-tree sizes within or among stands or among sample plots. Understanding the variation and dynamics of cavity trees has been hampered by the scarcity of data on a large scale (e.g., Allen and Corn 1990, Spetich 1995, Goodburn and Lorimer 1998).

Instead of estimating mean cavity-tree density, the Weibull model quantifies the probability for a range of cavity-tree abundances (Figures 1 and 2). A striking advantage of this approach is that cavity-tree abundance can be predicted for landscapes comprised of stands of varying size classes (or age classes) using simulation techniques that make repeated draws from the cavity-tree density probability distribution (Fan et al. 2004). If resource managers and planners have the information on the number of hectares by stand-size class or age class under different management alternatives, they can apply the results presented here to estimate the associated cavity-tree density and compare management alternatives (Fan et al. 2003a). This can be of great help in conservation planning and related decisionmaking.

For management applications, the cumulative probability distribution of cavity trees per hectare is a particularly useful display of the results. Whereas Figure 1 presents the probability of cavity-tree abundance for a given forest size (or age) class, the cumulative distribution (Figure 2) rearranges the same data to display the cumulative probability that a hectare in a given stand of a given size class will have less than the number of cavity trees shown on the x axis. In Figure 2, the cumulative probability distribution curves for all four size classes are plotted together to aid in comparisons among size classes. For example, if a manager is interested in maintaining at least 17 cavity trees/ha, the point where a vertical line at the target of 17 cavity trees/ha intersects the cumulative distribution curves indicates the probability that a hectare in the given size class will have fewer than the target of 17 cavity trees/ha. The probability of meeting or exceeding the target is one minus the probability of failure. For seedling stands, 92% of 1-ha samples are expected to have fewer than 17 cavity trees/ha; the corresponding probability that a given hectare in seedling stand will meet the target is 8%. In contrast, 19% of 1-ha plots in old-growth stands are expected to have fewer than 17 cavity trees, and 81% are expected to meet or exceed the 17-cavity-tree target. These probability models can be applied graphically to estimate cavity abundance by hectare for individual stands or automated make repeated random draws for each hectare of large landscapes comprised of stands of many size classes.

The cavity models presented here are based on ground-based cavity observations that inevitably overlook some actual cavities and cavity trees. Thus, the model makes conservative estimates of cavity-tree abundance (Healy et al. 1989, Jensen et al. 2002).

Table 2. The fitted parameters and standard errors of the Weibull function describing the frequency of cavity trees by diameter for various stand size classes. Also see Figures 1 and 2.

Stand size class[a]	Parameter	Estimate[b]	$Pr > F^c$
Seedling/sapling (stand age <30 years)	a	0.6875	<0.0001
	b	0.8663	
	c	–0.2832	
Pole (stand age 31–50 years)	a	0.8387	<0.0001
	b	2.3736	
	c	–0.1407	
Sawtimber (stand age 51–120 years)	a	1.4529	<0.0001
	b	3.5152	
	c	–2.3568	
Old-growth (stand age >120 years)	a	2.228	<0.0001
	b	7.1656	
	c	–0.8734	

[a] Age range is approximate for the stand size class in upland Central Hardwood forests.

[b] Parameter estimates for predicting the probability that a plot of a given size class will have x_t cavities per ha based on the model probability $= f(x_t) = a/b((x_t - c)/b)^{a-1}\exp[-((x_t - c)/b)^a](x_t = 0,1,2,\ldots)$
Values of x_t (0, 1, 2, 3, . . . 16) correspond to classes of cavity tree density (0, 0.1–10, 10.1–20, 20.1–30, . . . 150.1–160). Similarly the cumulative probability of having x_t or fewer cavities per ha for a stand of a given size class is found from the cumulative form of the Weibull function: cumulative probability $= F(x) = 1 - \exp[-((x_t - c)/b)^a]$

[c] Overall significance of the regression measured by the F-statistic.

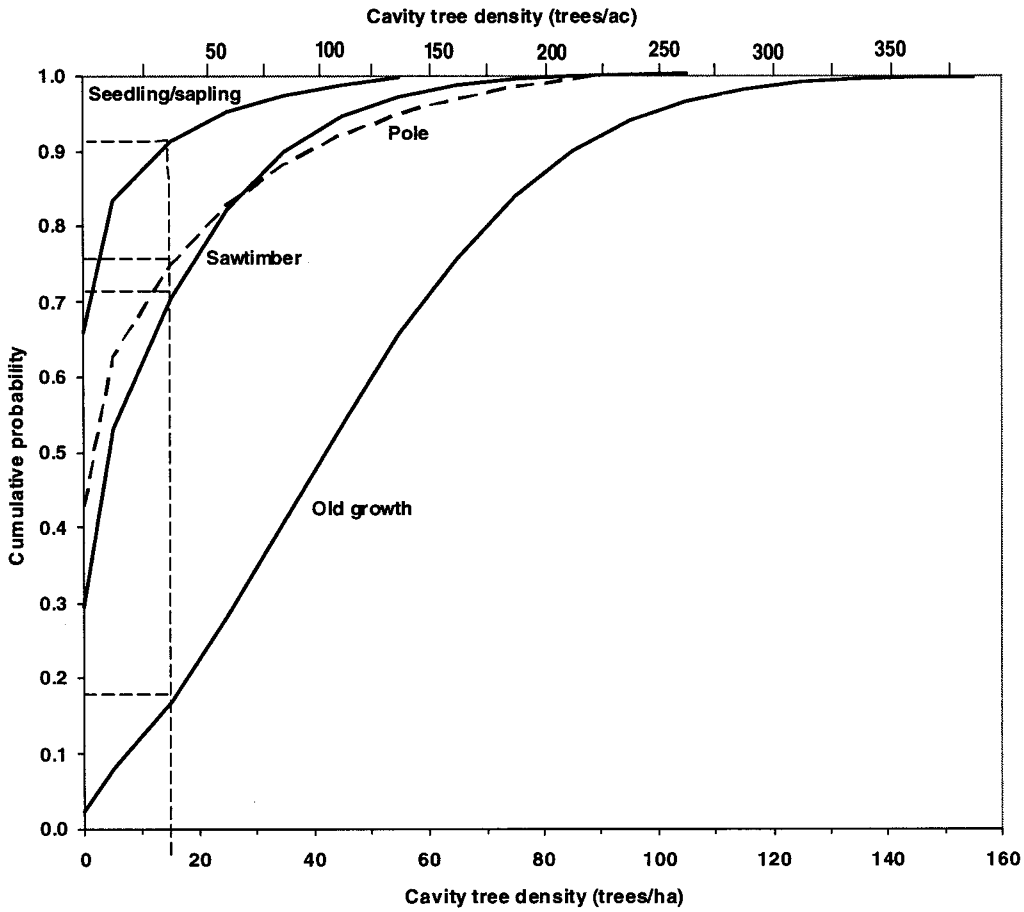

Figure 2. Cumulative probability that plots of the given size class will have fewer than the number of cavity trees indicated on the *x* axis. To facilitate reading and applying this graph, the probabilities were interpolated from class values (as shown in Figure 1) to display along a continuous *x* axis. As an example of how to use this graph, lines have been added to indicate probabilities that plots in the seedling/sapling, pole, sawlog, and old-growth size classes will have fewer than 17 cavity trees/ha (i.e., vertical line at 17 on *x* axis). Those probabilities are 0.92, 0.76, 0.73, and 0.19, respectively. The corresponding probabilities of 17 or more cavity trees/ha are 0.08, 0.24, 0.27, and 0.81, respectively. This graph can be readily applied to estimate whether or not a hectare in a given stand-size class (or age class) is likely to contain any specified number of cavity trees per hectare.

Table 3. The proportion of cavity trees by diameter class (and 95% confidence intervals) for stands of different size classes. For a given number of cavity trees in a stand of a given size class (e.g., from Figures 1 or 2), this is the proportion of those cavity trees that are likely to be in various dbh classes.

Stand size class[a]	Cavity tree dbh	Percent of Cavity trees	95% CI
Seedling/sapling (stand age <30 yr)	Small (13–25 cm)[b]	52	47–56
	Medium (26–48 cm)	40	36–45
	Large (>48 cm)	8	7–9
Pole (stand age 31–50 yr)	Small (13–25 cm)[b]	52	49–59
	Medium (26–48 cm)	40	37–43
	Large (>48 cm)	8	7–9
Sawtimber (stand age 51–119 yr)	Small (13–25 cm)[b]	40	37–42
	Medium (26–48 cm)	50	48–52
	Large (>48 cm)	10	10–11
Old-growth (stand age >120 yr)	Small (13–25 cm)[b]	37	34–39
	Medium (26–48 cm)	34	32–37
	Large (>48 cm)	29	27–31

[a] Age range is approximate for the stand size class in upland Central Hardwood forests.
[b] Trees smaller than 13 cm were not inventoried because few trees smaller than 13 cm have cavities useful to wildlife.

Seedling/sapling, pole, and sawtimber stands are usually distinguished during timber management because the size classes are indicative of current stand structure and future timber production. Those same size classes also are indicative of habitat quality for a variety of wildlife species (Thompson and DeGraaf 2001) because the stand-size classes differ significantly in cavity-tree abundance (Fan et al. 2003b). The Missouri Department of Conservation suggests 17 cavity trees/ha (2 large, 10 medium, and 5 small) for forest interior habitat for wildlife species (Titus 1983). Based on the frequency distribution of cavity trees (Figures 1 and 2, Table 2) the majority of second-growth forests do not meet this optimum level of cavity abundance. In the Central Hardwood Region, old-growth forests serve as important wildlife habitat and have received considerable attention because of their unique contributions to forest diversity at stand and landscape scales (e.g., Parker 1989, Shifley et al. 1995, 1997, Goodburn and Lorimer 1998, Spetich and Parker 1998, Fan et al. 2003b). Old-growth forests typically have far more cavity trees per hectare and larger cavity trees than second-growth forests (Figures 1 and 2, Table 2).

Estimates of the number of cavity trees per hectare are useful in wildlife habitat evaluation. More detailed habitat analyses will depend on knowledge of the number of cavity trees by cavity-size class. Cavity trees often have multiple cavities, and wildlife species vary in their cavity size requirements. In future studies, the results presented here could be readily supplemented with new data describing the cavity opening size and cavity frequency for trees of various size classes (e.g., based on tree size classes as in Table 3). In general, cavity data of all types are rare, and efforts to include cavity measurements in forest inventory procedures will extend opportunities for application and testing of cavity estimation procedures such as those described here.

Conclusions

As anticipated, seedling/sapling stands had the fewest cavity trees per hectare and old-growth stands had the most. Pole and sawtimber size stands had similar probabilities of cavity-tree abundance (Figure 1), but they differed in the size of the cavity trees (Table 3). Cavity trees in sawtimber stands were significantly larger than in pole stands. The values presented here, particularly for old-growth forests that encompass the upper limit of cavity-tree abundance, can serve as a reference for comparison to conditions in managed Central Hardwood forests.

A probability-based approach to estimating cavity-tree abundance provides the opportunity to quantify the high variability in cavity-tree abundance and use it to estimate the probability of achieving any target level of cavity-tree abundance. This procedure, which is based on grouping stands into broad size classes (or age classes) is compatible, with even relatively simple forest inventory systems. A graph of the cumulative probability of cavity abundance (Figure 2) is a particularly easy tool for managers to apply to estimate cavity abundance for individual stands or for groups of stands that comprise forest landscapes.

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