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FORAGING ECOLOGY OF PILEATED WOODPECKERS IN DUKES EXPERIMENTAL FOREST IN THE UPPER PENINSULA OF MICHIGAN

By

Michael R. Wierda

THESIS

Submitted to Northern Michigan University In partial fulfillment of the requirements For the degree of

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ABSTRACT

FORAGING ECOLOGY OF PILEATED WOODPECKERS IN DUKES EXPERIMENTAL FOREST IN THE UPPER PENINSULA OF MICHIGAN

By

Michael Ray Wierda

Pileated woodpecker selection of foraged trees was studied using a multiple spatial scale study in coniferous and deciduous forests in the Upper Penninsula of Michigan. Most previous works on pileated woodpecker foraging have been conducted in large homogeneous, contiguous tracts of forests of a single assemblage type. These studies found foraging preferences for stand type, tree type, and tree species; specifically, conifers in the western range, and deciduous trees in the eastern range. However, it was unclear if this selection resulted from availability because studied areas were dominated by preferred tree types and species or habitat data was not reported. The availability of suitable coniferous and deciduous assemblages in Dukes Experimental Forest in northern Michigan provided an opportunity to examine foraged tree selection with both habitat types present. Foraged trees were associated with a suite of characteristics: they were declining to moderately decayed (d.f. = 4, χ^2 = 10.29 and 297.38, respectively, P \leq 0.05), injured, and more had conks than expected (d.f. = 4, χ^2 = 360.05 and 644.08, respectively, $P \le 0.05$). Coarse examination of the data suggested that deciduous trees in general and aspens and yellow birch in particular were preferred. Further examination suggested that these trees were selected by pileated woodpeckers based on their characteristics alone, which are similar to characteristics of trees inhabited by carpenter ants, the primary prey of pileated woodpeckers.

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MICHAEL RAY WIERDA

DEDICATION

This thesis is dedicated to my parents Ron and Sue Wierda who always knew I had it in me.

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Following is a list of people and funding resources to which I would like to express great thanks. This is by no means an exhaustive list and to my family and friends who are not mentioned directly ... Thank You!

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This thesis follows the format prescribed by the American Psychological Association.

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INTRODUCTION

Pileated woodpeckers (Dryocopus pileatus) are an important habitat modifying species in late successional forest communities. These birds create large cavities in trees that provide feeding, roosting and nesting sites for many organisms and accelerate nutrient cycling and decomposition (Aubry & Raley, 2000; Aubry & Raley, 2002a; Aubry & Raley, 2002b; Bonar, 2000; Jackson & Jackson, 2004). Avian species using pileated woodpecker cavities for nests and roosts include the common merganser (Mergus merganser), American kestrel (Falco sparverius) and the hairy woodpecker (Picoides villosus; Aubry & Raley, 2002b). In addition, barred owls (Strix varia) nest almost exclusively in abandoned pileated woodpecker nests (Harestad & Keisker, 1989). Mammalian species also use pileated woodpecker cavities. Fishers (Martes pennati) use old nests for natal dens (Aubrey & Raley, 2002a), eastern gray squirrels (Sciurus carolinensis) and raccoons (Procyon lotor) used red-cockaded woodpecker (Picoides *borealis*) nests after pileated woodpeckers had increased the cavity size and entrance hole (Aubry & Raley, 2002b). Opportunistic foraging by hairy woodpeckers in relation to pileated woodpeckers has been observed (Maxson & Maxson, 1981). In that study at least three hairy woodpeckers foraged on a dead red oak (Quercus rubra) following the removal of bark by pileated woodpeckers, and one male hairy woodpecker and a pileated woodpecker foraged simultaneously.

Through foraging, nest construction, nest starts (i.e., nest cavities that were not completed) and roost construction, pileated woodpeckers accelerate decomposition and nutrient cycling of snags (standing dead trees), live trees and decadent trees. These processes are accelerated directly by the breaking apart of sound and decomposed wood

and indirectly by exposing interior wood of trees and snags to insects and fungal infection (Aubry & Raley, 2002b; Jackson & Jackson, 2004).

The current distribution of pileated woodpeckers covers the majority of the eastern third of the United States (U.S.), southern Canada, and portions of the Rocky and Cascade Mountains (Bohlen, 1989; Bull & Jackson, 1995; Peterjohn, 1989). Availability of suitable habitat is apparently a limiting factor for most populations of pileated woodpeckers (Bull & Jackson, 1995). The primary component defining suitable pileated woodpecker habitat is the presence of late successional forests, typically with trees \geq 50 cm in diameter at breast height (dbh) and high densities of snags (Bull, 1987; McClelland & McClelland, 1999; Mellen, Meslow, & Mannan, 1992).

The pileated woodpecker's diet consists mainly of insects (primarily carpenter ants, *Camponotus* spp.), wild fruits and nuts. Excavating deep into the tree, scaling bark off the surface and surface pecking are three foraging behaviors used by pileated woodpeckers (Bull, 1987; Bull & Holthausen, 1993; Conner, 1981). Excavation foraging into the interior of trees is the pileated woodpecker's primary means of obtaining food (Bull, 1987; Bull & Holthausen, 1993; Flemming, Holloway, Watts, & Lawrance, 1999). Pileated woodpeckers remove large slivers of wood to gain access to carpenter ant galleries, creating highly visible rectangular cavities. A long extensible tongue with barbs and sticky saliva is then used to extract ants from tunnels within the wood (Bull & Jackson, 1995). Foraging often occurs in stands \geq 40 years old with trees and snags \geq 50 cm dbh and on down trees, and stumps of similar size (Bull, 1987; Conner, Hooper, Crawford, & Mosby, 1975; Mellen et al., 1992).

Studies of pileated woodpecker ecology in its western range in Oregon and western Montana, have documented a strong preference for nearly exclusive usage of coniferous species (Bull, 1987; Bull & Holthausen, 1993; McClelland & McClelland, 1999). Studies in the eastern range in southern Québec and Virginia showed preferences for deciduous species and shade tolerant hardwood assemblages (Conner, 1981; Savignac, Desrochers, & Huot, 1994). However, whether this indicates a foraging preference is unclear because western study areas and eastern study areas were dominated by coniferous and deciduous species, respectively (Bull, 1987; Conner et al., 1975).

Intra-community preferences for tree characteristics in coniferous forests and deciduous forests (e.g., dbh, tree species, stand composition, height, and level of decay) have been demonstrated (Bull, 1987; Flemming et al., 1999; Savignac et al., 2000). In coniferous forests of the north western U.S., foraged tree dbhs were on average ≥ 30 cm (Bull, 1987; Bull & Holthausen, 1993; Bull & Meslow, 1977). In New Brunswick, Canada, the median dbh of foraged trees was 27 cm (Flemming et al., 1999). Bonar (1999) suggested that clusters of more than 8 snags \geq 16 cm dbh per ha, resulted in optimal conditions for pileated woodpecker foraging. Flemming et al. (1999) demonstrated that red spruce (*Picea rubens*) was used more frequently in contiguous coniferous dominated forests while deciduous species were used more frequently in fragmented mixed forests. Flemming et al. (1999) suggested that preference for deciduous trees in the fragmented forest may have simply been a preference for larger trees, because, in the fragmented forests larger coniferous trees had been removed. Flemming et al. (1999) found that the intensity of foraging on dead and declining balsam firs (Abies balsamea) was negatively correlated with availability. Lack of suitably sized

trees of this preferred species was thought to have forced pileated woodpeckers to use greater portions of the available balsam firs (Flemming et al., 1999). Flemming et al. (1999) argued that pileated woodpeckers preferred red spruce and balsam fir because the bark loosened relatively rapidly once dead and because the wood was softer than shade tolerant hardwood species. However, Savignac et al. (2000) reported that highly decomposed large firs in similar low densities were not preferred over large shade tolerant hardwood snags. In eastern Canada, pileated woodpeckers preferred large yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), and balsam firs in mature shade tolerant hardwood stands, but firs were more frequently used than hardwoods in immature mixed shade-intolerant stands (Savignac et al., 2000). Flemming et al. (1999) reported a significant difference in heights between foraged trees and available trees. Foraged trees were generally shorter than available trees, typically due to a heightened state of decay. Foraged trees were characterized as dead with a broken top, while the average available tree was characterized as live.

Previous studies of foraging site selection by pileated woodpeckers were done in landscapes with relatively large, homogeneous, contiguous tracts of one habitat type. In predominantly coniferous habitats (west coast studies) and in predominately deciduous habitats (mid-west and east coast studies), fundamentally different foraged tree selection occurred (Bull, Holthausen, & Henjum, 1992; Conner & Crawford, 1974; Mannan, 1984; McClelland & McClelland, 1999). These differences were correlated to the predominant assemblages in the study areas.

The availability of suitable coniferous and deciduous assemblages in the upper peninsula of Michigan and the mosaic arrangement of these assemblages provided an

opportunity to examine pileated woodpecker foraging when both suitable deciduous and coniferous habitats were available. The forests of the upper peninsula Michigan are transitional zones between northern deciduous and northern coniferous forests with mature (60-70 years old) and climax (\geq 100 year) patches of deciduous and coniferous assemblages (Wolford, 2002). Sugar maple and eastern hemlock (*Tsuga canadensis*) were the most common tree species in the mature to climax forests of the upper peninsula of Michigan (Wolford, 2002). Pileated woodpecker foraging signs have been noted on both of these species (personal observation) and foraging on sugar maples has been documented (Flemming et al., 1999).

This study was designed to examine pileated woodpeckers' foraging site selection 1) at the stand level (i.e., are deciduous or mixed assemblages preferred), 2) at the tree type level (i.e., are deciduous or coniferous trees preferred), 3) at the tree species level (i.e., are any tree species preferred), and 4) at the tree characteristic level (i.e., are any tree characteristics correlated with foraging). This study is representative of pileated woodpecker fall and winter foraging preferences. Pileated woodpeckers typically forage on the ground during the summer because carpenter ants have moved out of trees and into tunnels under leaf litter. Carpenter ants move back into trees for the fall and winter (unpublished data per comm. Savignac, 2005).

MATERIALS AND METHODS

Study Area

The research was conducted in Dukes Experimental Forest (2201 ha) in the upper peninsula of Michigan. Dukes Experimental Forest is located in the Hiawatha National

Forest in Marquette County Transects 46 and 45 N. Range 23 W. Dukes Experimental Forest contains mature deciduous assemblages and mature mixed assemblages. Mixed assemblages were composed of a 1:1 ratio of deciduous and coniferous trees. In the mixed assemblages, sugar maples and eastern hemlocks co-dominated. In the mature deciduous assemblages, sugar maples dominated the available trees.

Sampling Methods

Mature/climax mixed and deciduous assemblages were selected from a National Forest Service stand survey map. Selected assemblages were at least 40 m x 500 m. Within each assemblage, one to four "ribbon plots" were established. Ribbon plots were 30 m wide, 400 m long and spaced a minimum of 30 m apart (Figure 1a, b). Ten mixed and 12 deciduous ribbon plots were established. Systematic searches of ribbon plots were conducted from May to September 2004. Starting at a corner and walking the plot boundary, trees inside the ribbon plot were scanned for subcambial excavation foraging sites (SEFS). At 25 m intervals, a full 360° was scanned for SEFS (Figure 1b, c). Data were collected on all current and recent SEFS. Current and recent foraging was indicated by the presence of woodchips on top of the leaf litter from the previous fall. When the line of vision was obscured (generally in dense hemlock stands), a third pass was made up the middle of the ribbon plot. The same scanning technique was used. If SEFS were spotted outside of the plot during ribbon plot searches, the same data were collected.

The location of each SEFS was recorded with a global positioning system, and its characteristics were recorded. Subcambial excavation foraging site characteristics included: location, plot type, tree species, dbh, tree/snag height, foraging location (maximum height), decay class, presence or absence of injury (e.g., fire, lightning, frost

crack, forked top, broken top), presence or absence of conk, canopy height, and canopy cover. Mutually exclusive decay classes were defined:

- Decomposed snags_(DC): No branches, stem very punky or rotten, bark mostly gone.
- Loose Bark snags_(DC): few or no branches, stem mostly intact but may be starting to soften, bark loose and easily removed.
- Recently dead trees_(DC): fine branches gone, major branches still present, stem mostly sound.
- Declining trees_(DC): fine branches still present, major branches mostly present, often one or more major branches had brown or no needles or leaves.
- Live trees_(DC): all remaining standing trees that do not fit the above categories.

Characteristics of trees available for foraging were estimated by subsampling ribbon plots. Each ribbon plot was divided into sixteen equal blocks and three blocks were selected using a random number generator (Microsoft Excel®). Within each selected block, a 15 m radius habitat plot was centered. For all snags and trees with a dbh \geq 6.36 cm, plot type, tree species, dbh, decay class, presence or absence of injury, and conk were recorded. Red and sugar maple (*Acer rubrum* and *A. saccharum*, respectively), black and white spruce (*Picea mariana* and *P. glauca*, respectively) and quaking and big tooth aspen (*Populus tremuloides* and *P. grandidentata*, respectively) trees were grouped into maples, spruces, and aspens because some individual trees could not be identified to the species level.

Statistical Methods

The proportion of trees foraged inside the plots and the proportion of trees foraged outside the plots were compared for deciduous plots and mixed plots combined to determine if data sets (i.e., trees foraged inside ribbon plots and trees foraged outside ribbon plots) could be pooled. The numbers of available trees were estimated based on the number of habitat trees and the differences in search areas. Because the proportion of trees foraged inside ribbon plots was different from the proportion of trees foraged outside ribbon plots; stand type, tree type, and tree species proportion analyses used only inside ribbons plot data. Proportions were compared using a normal approximation of a continuity-corrected chi-square (χ_c^2) test (Zar, 1999).

Tree characteristic analyses used all applicable foraged trees ($n \le 120$) and all applicable habitat trees (i.e., non foraged trees ≥ 6.36 cm dbh, $n \le 3155$). Tree characteristics were selected from past pileated woodpecker foraging, nesting, and roosting literature. Because these characteristics previously had been correlated with pileated woodpecker habitat possible colinearity between variables was investigated.

To investigate how much variables interacted, five variables previously correlated with foraged trees were considered post-hoc. They were: presence of injury (injury), presence of fungal infection (conk), decay class of the tree (decay), dbh, and tree species (spp). These variables were chosen because of previously published correlations with pileated woodpecker foraged tree selection (Bull et al., 1992; Conner & Crawford, 1974; Flemming et al., 1999; Mannan, 1984; McClelland & McClelland, 1999; Savignac et al., 2000). Injury and conk were analyzed as 0-1 variables indicating absence (0) or presence (1) of the characteristic. Decay was analyzed in a collapsed form based on the results of

preliminary analysis. Because dead and loose bark decay classes did not demonstrated statistically significant differences in the preliminary analysis, they were collapsed into a single category, resulting in four values for the decay variable: (0) live, (1) declining, (2) dead/loose bark, and (3) decomposed. Three tree species (Aspen, Yellow Birch, and Eastern Hemlock) were included in this investigation based on results of preliminary analysis. An indicator variable was created for each species (indicating absence (0) or presence (1)).

Tests of colinearity were conducted between all combinations of individual tree characteristic variables and categorical variables for tree species to determine if any variables were too closely related to be meaningfully combined as interaction variables. Ordinal variable pairs with Kendall's tau-b correlations of greater than 0.80 (i.e., > 64% of variance shared) were considered too closely related to be meaningfully combined for further analysis regarding variable interaction (Table 1). To further test whether tree characteristics or tree species were driving foraging selection, a logistic regression model was constructed with interaction variables (Table 2, Hosmer, 1989). The null hypothesis was that coefficients for tree characteristic interaction variables were as likely to be zero as coefficients including species indicator variables.

In general, contingency table analyses were used to determine if the frequency of one variable was independent of the frequency of a second variable. Because average expected count was always > 6, contingency tables were analyzed with the chi-square statistic (Zar, 1999). If variables were not independent, post-hoc chi-square tests were conducted to determine which observed counts deviated significantly from expected counts. Bonferroni's corrections were used to avoid alpha inflation in the post-hoc chi-

square tests. Student's t-test was used to compare averages where applicable. Pair-wise comparisons between proportions of foraged tree species were made for each individual tree species using the Dunnett test statistic (Zar, 1999). For a summation of all statistical tests conducted see appendix A. An alpha of 0.05 was used as the criterion for rejection of null hypothesis.

RESULTS

Total areas surveyed for foraged trees inside (n = 40) and outside (n = 25) of 12 deciduous plots were 144,000 m² and 274,802 m², respectively. Total areas surveyed for foraged trees inside (n = 28) and outside (n = 27) of 10 mixed plots were 120,000 m² and 316,726 m², respectively. One-hundred deciduous and 20 coniferous foraged trees were characterized in total. Two thousand and twenty non-foraged deciduous trees and 935 non-foraged coniferous trees were characterized during habitat surveys. The total area of habitat surveyed in deciduous plots and in mixed plots were 25,446.96 m² and 16,964.64 m², respectively.

Tests for colinearity between ordinal variables did not result in the exclusion of any variable combinations. Although significant correlations existed between all combinations (P < 0.05), none of the variables attained the rejection level of 64% shared variance (Kendall's tau-b = 0.80). Maximum shared variance was 27% (Kendall's tau-b = 0.52) between conk and decay (Table 1).

In the final regression model, five interaction variables met the criteria for model retention. They were DBH by Decay, DBH by Injury, Injury by Decay, Injury by Conk, and Conk by Decay, listed here in increasing order of significance for the score statistic.

The full model explained approximately 57.3% of the variance as approximated by Negelkerke's R Square. This model included all but one of the variables from the individual tree characteristic subset. No species indicator variables met the criteria for inclusion in the model. These results suggest that the null hypothesis should be rejected.

Mean dbh of foraged trees (45.16 cm, n = 100) was greater than the mean dbh of non-foraged trees (20.80 cm, n = 2220, P < 0.001). Foraging was not independent of decay class (d.f. = 4, χ^2 = 670.99, P < 0.001; Table 3). Foraged trees had fewer live trees_(DC) and more declining trees_(DC), dead trees_(DC) and loose bark snags_(DC) than expected (d.f. = 1, χ^2 = 81.20, 10.29, 297.38 and 256.87, respectively, P ≤ 0.05). Non-foraged trees had fewer dead trees_(DC) and loose bark snags_(DC) than expected (d.f. = 1, χ^2 = 11.28 and 9.63, respectively, P ≤ 0.05).

Foraging was not independent of injuries and conks (d.f. = 1, χ^2 = 457.50 and 702.78 respectively, P < 0.001; Tables 4 and 5, respectively). Foraged trees had fewer trees without injuries and conks and more trees with injuries and conks than expected (d.f. = 1, χ^2 = 81.66, 38.03, 360.05 and 644.08, respectively, P < 0.05). Non-foraged trees had fewer trees with injuries and conks than expected (d.f. = 1, χ^2 = 13.96 and 22.96 respectively, P < 0.05).

Proportionately more trees were foraged inside plots (68/19,706.90) than were foraged outside plots (52/44,055.80; $Z_C = 6.01$, P < 0.001). Thus, only inside plots data were used for stand type, tree type, and tree species proportion analyses.

The proportion of trees foraged in deciduous plots (40/12,562.6) was equal to the proportion of trees foraged in mixed plots (28/6,613.76; $Z_C = 1.03$, 0.20 < P < 0.50; Table 6). Mean dbh of trees in deciduous plots (21.65 cm, n = 1810) was equal to the

mean dbh of trees in mixed plots (20.79 cm, n = 1465, 0.05 < P < 0.10). Plot type was not independent of decay class (d.f. = 4, χ^2 = 15.26, 0.001 < P < 0.005; Table 7). Deciduous plots had fewer live trees_{DC} than expected (d.f. =1, χ^2 = 4.22, P ≤ 0.05). However, frequency of trees with injury and conk was independent of plot type (d.f. = 1, and 1, χ^2 = 1.97 and 0.75, 0.10 < P < 0.25 and 0.25 < P < 0.50, respectively; Table 8 and 9).

The proportion of deciduous trees foraged (57/11,306.73) was approximately 4.2 times greater than the proportion of coniferous trees foraged (11/9,147.20; $Z_C = 4.62$, P < 0.001; Table 10). The mean dbh of deciduous trees (21.85 cm, n = 2320) was larger than the mean dbh of coniferous trees (19.85 cm, n = 955; P < 0.001). Tree type was not independent of decay class (d.f. = 4, χ^2 = 58.79, P < 0.001; Table 11). Deciduous trees had more declining trees_{DC}, and loose bark snags_{DC}, (d.f. = 1, χ^2 = 6.28 and 6.52, respectively, $P \le 0.05$). Coniferous trees had fewer declining trees_{DC}, and loose bark snags_{DC} (d.f. = 1, χ^2 = 15.28 and 15.83, respectively, P \leq 0.05). Frequencies of injured trees differed with tree type (d.f. = 1, χ^2 = 37.25, P < 0.001; Table 12). Deciduous trees had more trees with injuries than expected (d.f. = 1, $\chi^2 = 8.84$, P ≤ 0.05). Coniferous trees had fewer trees with injuries than expected (d.f. = 1, $\chi^2 = 21.49$, P ≤ 0.05). Frequencies of trees with conks differed with tree type (d.f. = 1, χ^2 = 43.45, P < 0.001; Table 13). Deciduous trees had more trees with conks than expected (d.f. = 1, $\chi^2 = 11.98$, $P \le 0.05$). Conifers had fewer trees with conks than expected (d.f. = 1, $\chi^2 = 29.07$, $P \le 0.05$).

Foraging was not independent of tree species (d.f. = 15, χ^2 = 180.70, P < 0.001; Table 14). Aspens, yellow birch, white cedar, and white pine had significantly more foraged trees than expected (d.f. = 1, χ^2 = 73.50, 59.82, 11.22, and 6.4, respectively, P ≤ 0.05). Eastern hemlock had significantly fewer foraged trees than expected (d.f. = 1, χ^2 = 10.41, P ≤ 0.05).

Aspens were foraged in significantly greater proportions than all other tree species ($P \le 0.05$). Yellow birch was foraged in significantly greater proportion than eastern hemlock, balsam fir and maples ($P \le 0.05$). Maples and spruces were foraged in significantly greater proportions than eastern hemlock ($P \le 0.05$). Aspens mean dbh (32.89 cm, n = 42) compared to all other species (21.11 cm, n = 3233) was significantly larger (P < 0.001). Yellow birch (29.77 cm, n = 292) mean dbh compared to eastern hemlock, balsam fir and maples (20.32 cm, n = 2569) was significantly larger (P < 0.001). Maple (20.98 cm, n = 1761) and spruce (18.83 cm, n = 67) mean dbhs were significantly smaller than eastern hemlock (21.55 cm, n = 605; 0.20 < P < 0.50 and 0.02 < P < 0.05, respectively).

Tree species was not independent of decay class (d.f. = 60, χ^2 = 338.47, P < 0.001; Table 15). Aspens had fewer live trees_{DC} and more loose bark snags_{DC} than expected (d.f. = 1, χ^2 = 9.56 and 72.90, respectively, P ≤ 0.05). Yellow birch had fewer live trees_{DC}, more dead trees_{DC}, more loose bark snags_{DC}, and more decomposed snags_{DC} than expected (d.f. = 1, χ^2 = 11.50, 22.67, 11.53, and 44.00, respectively, P ≤ 0.05). Maples had fewer decomposed snags_{DC} than expected (d.f. = 1, χ^2 =9.12, P ≤ 0.05). Eastern hemlock had more live trees_{DC}, fewer declining trees_{DC}, fewer dead trees_{DC}, and more loose bark snags_{DC} than expected (d.f. = 1, χ^2 = 8.91, 13.05, 10.53, and 26.01, respectively, P ≤ 0.05). Spruces had more decomposed snags_{DC} than expected (d.f. = 1, $\chi^2 = 10.68$, P ≤ 0.05), and black locust had more declining trees_{DC} than expected (d.f. = 1, $\chi^2 = 31.34$, P ≤ 0.01).

Frequency of injured trees differed among tree species (d.f. = 15, χ^2 = 291.44, P < 0.001; Table 16). Aspens and yellow birch both had fewer trees without injuries and more trees with injuries than expected (d.f = 1, χ^2 = 15.73, 22.34 and 69.05, 98.23, respectively, P ≤ 0.05). Eastern hemlock had more trees without injuries and fewer trees with injuries than expected (d.f. = 1, χ^2 = 6.14 and 27.01, P ≤ 0.05). Balsam fir had fewer trees with injuries than expected (d.f. = 1, χ^2 = 11.29, P ≤ 0.05). Black walnut had fewer trees with injuries than expected (d.f. = 1, χ^2 = 6.40, P ≤ 0.05).

Frequency of trees with conks differed among tree species (d.f = 15, χ^2 = 364.07, P < 0.001; Table 17). Aspens and yellow birch had fewer trees without conks (d.f. = 1, χ^2 = 5.58 and 12.20, respectively, P ≤ 0.05) and more trees with conks than expected (d.f. = 1, χ^2 = 93.95 and 206.22, respectively, P ≤ 0.05). Maples and eastern hemlock had fewer trees with conks than expected (d.f. = 1, χ^2 = 5.14 and 19.78, respectively, P ≤ 0.05).

Mixed plots

Mixed plots consisted of 49.9% deciduous species and 50.1% coniferous species. Thirty-eight foraged deciduous and 17 foraged coniferous trees were characterized in total. Six hundred ninety-three non-foraged deciduous trees and 717 non-foraged coniferous trees were characterized during habitat surveys. The proportion of deciduous trees foraged (38/4,939.96) was approximately 2.3 times greater than the proportion of coniferous trees foraged (17/5,088.73; P = 0.14; Table 18). In contrast to that of all plots (pooled mixed and deciduous plots), mean dbh of deciduous trees (20.88 cm, n = 731) was not significantly different from the mean dbh of coniferous trees (20.69 cm, n = 734; P = 0.79).

The same pattern emerged in mixed plots as was reported in all plots. Foraging was not independent of decay class (d.f = 4, χ^2 = 299.04, P < 0.001; Table 19). Non-foraged trees had fewer loose bark trees_{DC} than expected (d.f. = 1, χ^2 = 6.64, P ≤ 0.05), and foraged trees had fewer live trees_{DC}, more dead trees_{DC} and loose bark snags_{DC} than expected (d.f. = 1, χ^2 = 32.87, 79.75 and 176.04, respectively, P ≤ 0.05).

Foraging was not independent of injuries and conks (d.f. = 1, χ^2 = 175.08 and 335.66, respectively, P < 0.001; Tables 20 and 21). Foraged trees had fewer trees without injuries and conks and more trees with injuries and conks than expected (d.f. = 1, χ^2 = 33.01, 19.53, 135.11 and 308.00, respectively, P < 0.001), and non-foraged trees had fewer trees with injuries and conks than expected (d.f. = 1, χ^2 = 5.28 and 11.24, respectively, P < 0.05).

Tree type was not independent of decay class, injury or conk (d.f., 4, 1, and 1, $\chi^2 = 33.66, 31.60$ and 43.79, respectively, P < 0.001; Tables 22, 23, and 24). Deciduous trees had more declining trees_{DC}, more loose bark snags_{DC}, more trees with injuries, and more trees with conks (d.f. = 1, $\chi^2 = 6.26, 6.34, 12.72$ and 20.63, respectively, P ≤ 0.05) and coniferous trees had fewer declining trees_{DC}, fewer loose bark trees_{DC}, fewer trees with injuries and fewer trees with conks than expected (d.f. = 1, $\chi^2 = 6.26, 6.31, 12.69$ and 20.54, respectively, P ≤ 0.05). In contrast to deciduous trees in all plots, deciduous trees had fewer live trees_{DC} than expected (d.f. = 1, $\chi^2 = 17.25$, P ≤ 0.05).

Foraging was not independent of tree species (d.f. = 8, χ^2 = 93.82, P < 0.001; Table 25). As reported for all plots above: aspens, yellow birch and white pine had significantly more foraged trees than expected (d.f. = 1, χ^2 = 18.68, 46.61, and 6.40, respectively, P \leq 0.05), and eastern hemlocks had significantly fewer foraged trees than expected (d.f. = 1, χ^2 = 8.98, P \leq 0.05).

Contingency table analyses showed that the tree species was not independent of decay class (d.f. =32, $\chi^2 = 258.12$, P <0.001; Table 26). Aspens had more loose bark snags_{DC} than expected (d.f. = 1, $\chi^2 = 105.30$, P ≤ 0.05), yellow birch had fewer live trees_{DC}, more dead trees_{DC} and more decomposed snags_{DC} than expected (d.f. = 1, $\chi^2 = 6.08$, 12.89 and 17.38, respectively, P ≤ 0.05), eastern hemlock had more live trees_{DC}, fewer declining trees_{DC}, fewer dead trees_{DC} and fewer loose bark snags_{DC} than expected (d.f. = 1, $\chi^2 = 6.00$, 6.25, 8.50 and 19.40, respectively, P ≤ 0.05), maples had fewer decomposed snags_{DC} than expected (d.f. = 1, $\chi^2 = 6.00$, 6.25, 8.50 and 19.40, respectively, P ≤ 0.05), and spruces had significantly more decomposed snags_{DC} than expected (d.f. = 1, $\chi^2 = 7.65$, P ≤ 0.05). In contrast to these tree species in all plots, yellow birch had more loose bark snags_{DC} than expected (d.f. = 1, $\chi^2 = 5.63$, P ≤ 0.05), and balsam fir had more loose bark snags_{DC} and decayed snags_{DC} (d.f. = 1, $\chi^2 = 5.98$ and 10.88, respectively, P ≤ 0.5).

Tree species was not independent of injury (d.f. = 8, χ^2 = 168.05, P < 0.001; Table 27). Aspens and yellow birch had fewer trees without injuries (d.f. = 1, χ^2 = 9.89 and 13.00, respectively, P ≤ 0.05) and more trees with injuries than expected (d.f. = 1, χ^2 = 40.57 and 53.33, respectively, P ≤ 0.05), eastern hemlock had more trees without injuries and fewer with injuries than expected (d.f. = 1, χ^2 = 7.07 and 295.35, respectively, P ≤ 0.05).

Tree species was not independent of conk (d.f. = 8, χ^2 = 194.59, P < 0.001; Table 28). Aspens had more trees with conks than expected (d.f. = 1, χ^2 = 60.17, P ≤ 0.05),

yellow birch had fewer trees without conks and more trees with conks than expected (d.f. = 1, χ^2 = 6.22 and 96.53, respectively, P ≤ 0.05), and eastern hemlock had fewer trees with conks than expected (d.f. = 1, χ^2 = 16.79, P ≤ 0.05).

Tree species were not foraged equally. Aspens and yellow birch were foraged in significantly greater proportions than eastern hemlock, maples, spruces and balsam fir ($P \le 0.05$). White cedar was foraged in significantly greater proportions than eastern hemlock and maples ($P \le 0.05$). Aspen and yellow birch mean dbh (27.95 cm, n = 178) were significantly larger than eastern hemlock, maples, spruces, and balsam fir (19.22 cm, n = 1184, P < 0.001). White cedar mean dbh (28.22 cm, n = 68) was significantly larger than eastern hemlock and maples (19.81 cm, n = 1037; P < 0.001).

DISCUSSION

In Dukes Experimental Forest pileated woodpeckers appeared to select for foraged trees based on tree type (deciduous trees), tree species (aspens and yellow birch) and tree characteristics (decay class, injury and conk). However, these selections were associated with a suite of tree characteristics. In general, foraged trees/snags were declining to moderately decayed, injured and had conks. Proportionately more deciduous trees, which were foraged more than coniferous trees, followed this general trend as did the highly foraged aspens and yellow birch.

Savignac et al. (2000) reported in southern Quebec that pileated woodpeckers avoided coniferous stands and preferred "mature mixed shade-tolerant hardwood stands" for foraging. Pileated woodpeckers in Dukes Experimental Forest used mixed stands and deciduous stands equally. Savignac et al. (2000) suggested that the negative relationship

between foraging and coniferous stands was possibly due to the lack of high quality trees for foraging (e.g., large yellow birch, sugar maple and balsam fir). Sugar maple and yellow birch were the highly foraged species in the mature and over mature shadetolerant hardwood stands in southern Quebec, while balsam fir was the highly foraged species in the immature mixed shade-intolerant stands. The coniferous stands in their study were actually coniferous plantations that were < 30 years old. The next closest stand age in the study was 10 - 50 year old stands (Savignac et al., 2000). Thus, it is possible that coniferous stands were avoided because of their characteristics (i.e., they were younger than other stands in the study) and potential habitat for pileated woodpecker's food sources (i.e., carpenter ants and bugs in dead and down wood), may have been removed for ease of planting and future harvesting. The findings in Dukes Experimental Forest support the hypothesis of selection based on characteristics. Unfortunately, characteristic profiles for individual stand types were not reported by Savignac et al. (2000).

Flemming et al. (1999) reported that deciduous trees were foraged more than coniferous trees (33.6% vs. 12.9%, respectively) in the fragmented forests of New Brunswick, Canada. They also reported that deciduous trees in the fragmented forests were more decayed and injured more often than the conifers. Pileated woodpeckers in Dukes Experimental Forest foraged similarly. Selection of deciduous trees in Dukes Experimental Forest was associated with three tree characteristics: declining to moderately decayed and trees with injuries, and conks. This suggests that deciduous trees were selected according to state of decay and presence of injury. Bunnel, Houde, Johnston & Wind (2002) reported that coniferous trees in the Pacific Northwest were

avoided until they reached a suitable decay class (recently dead), and with further decay their attractiveness as foraging sites increased.

Bull & Meslow (1977) reported that Douglas fir and larch were selected for while ponderosa pine was selected against. Bull (1987) reported preferences for ponderosa pine, Douglas fir and western larch. These studies were conducted in two sites in the Blue Mountains in north east Oregon. The selection against ponderosa pine in 1977 and then selection for in 1987 suggests that selection is not based on species. Ponderosa pines in 1977 may not have reached suitable levels of decay for carpenter ants to be present, and thus were not foraged by pileated woodpeckers. While pileated woodpecker foraging was distributed in Dukes Experimental Forest in a way that could suggest selection and avoidance according to tree species, selection of forage trees and avoidance of non-forage trees correlate well with tree characteristics. Trees with injuries, fungal growth, and signs of more advanced decay (i.e., aspen and yellow birch) were foraged more than expected while trees without injuries, fungal growth, and signs of slight decay (i.e., eastern hemlock) were foraged less than expected. Thus, these species followed the characteristic trends of foraged and non-foraged trees.

Five species of trees were foraged significantly more than other species. For two of these species, aspens and yellow birch (which were foraged more than expected and more than most other species), it was the characteristics of the more foraged species which influenced selection (Figures 3 and 4). Maples, spruces and white cedar were foraged according to availability and were foraged significantly more than eastern hemlock only. Eastern hemlock was the only species of tree in the study foraged significantly less than expected (Figure 5). Thus, aspens and yellow birch are the best

representatives of foraged trees, and eastern hemlock is the best representative of nonforaged tree species in Dukes Experimental Forest.

Bull (1987) reported that live trees were foraged almost as often as dead trees. However, the majority of the foraging activity on live trees was scaling, not subcambial excavation foraging. In the Dukes Experimental Forest study, subcambial excavation foraging cavities were used to identify pileated woodpecker foraging activity and actual foraging activities were not observed. Therefore, the importance of live trees may have been underestimated. Bull (1987) reported that pileated woodpeckers foraged on larger recently dead trees (within 5 years). Bull & Holthausen (1993) reported that snags \geq 38 cm dbh were preferred. In Dukes Experimental Forest, foraged trees (median = 43.6 cm, range = 7.95 cm to 85.31 cm) were larger than non-foraged trees (median = 16.23 cm, range = 2.23 cm to 91.35 cm). However, dbh data was not separated into size classes for the Dukes Experimental Forest study, and thus a preference for a specific size is not reported. Savignac et al. (2000) reported a positive association between pileated woodpecker foraging and density of small (≤ 30 cm) snags and large (≥ 31 cm) snags, and a negative association for small live trees (≤ 30 cm). This suggests that while tree size is associated with foraged trees, the physical state of the tree (i.e., decay class) is more important. Bunnell et al. (2002) reported that decay state may reflect the likelihood of hosting carpenter ants, and size of tree may not influence feeding preference.

Large trees are older, and thus have more potential for injury simply due to exposure. Injuries make trees more likely to have fungal heart rot via exposure of the sap wood, and carpenter ants are more likely to have colonies in trees with heart rot (Farris,

Martin & Zack, 2004; Jackson & Jackson, 2004; McClelland & McClelland, 1999; Sanders, 1964).

Carpenter ants create tunnels in decomposed cores of trees which start at the bole and typically extend up the tree, sometimes invading sound wood (Conners et al., 1975; Sanders, 1964). Sanders (1964) reported that the majority of carpenter ant galleries were correlated with slight fungal decay rather than extensive fungal decay. Foraged trees in Dukes Experimental Forest were declining to moderately decayed.

Fungal infection of trees improves habitat for pileated woodpeckers directly and indirectly. Directly it results in the softening of heartwood and loosening of bark thus making excavation foraging easier. Indirectly it creates highly suitable habitat for carpenter ants (Sanders, 1964). In this study, the presence of conks was used as the indicator of fungal infection. Thus, the presence of heart-rot fungus was probably underestimated. Jackson & Jackson (2004) reported that heart-rot fungi may grow unnoticed in a tree for several years before conks appear on the surface.

Injuries exposing the interior of the tree to the environment increase the likelihood of heart rot (Bull et al., 1992). Farris et al. (2004) reported that wood-inhabiting fungi were isolated from woodpecker bills at greater frequencies than expected at random. Thus, pileated woodpeckers may also promote fungal invasion of sapwood by physically creating injuries that expose the interior of the tree and by acting as vectors for wood decomposing fungal spores, yeast cells, or hyphae (Farris et al., 2004).

CONCLUSIONS

This study has potentially underestimated three things: first, the importance of live trees as food sources, second, the importance of decomposed trees as food sources, and third the occurrence of fungal infection in foraged trees.

In Dukes Experimental Forest, a suite of characteristics were associated with pileated woodpecker foraged trees. Coarser examination of the data suggested that deciduous trees and two species in particular (aspens and yellow birch) were being selected. However, this analysis suggested trees were selected due to their characteristics.

Interactions between characteristics such as size, exposure of heartwood (i.e., injury), and extent of fungal infection demonstrated the strongest associations to foraged trees and have a strong ecological bases. Tree size is likely indirectly correlated through carpenter ant and heart-rot fungus ecology. The two levels of decay most strongly associated with foraged trees (declining and dead) showed high injury and conk rates. Rates for conks were higher in foraged trees also, and even so, probably underestimated the presence of fungal infection. Because 1) carpenter ants make up the majority of the pileated woodpeckers diet, 2) trees with fungal infections are highly suitable habitats for carpenter ants, and 3) trees need to reach a suitable level of decay to be attractive as pileated woodpecker foraging sites, decay class is an important characteristic related to foraged tree selection. The selection of foraged trees is probably also directly related to the extent of fungal infection. Because injuries expose the interior of the tree to the environment increasing the likelihood of heart rot and pileated woodpeckers promote fungal infection injuries and acting as vectors for wood decomposing

fungal spores, injury is an important characteristic in foraged tree selection. Thus, fungal infection seems to be the ultimate basis for pileated woodpecker foraged tree selection. While decay class is an important characteristic related to foraged tree selection, it is unrealistic to separate it from the occurrences of injuries or conks because all three are intimately related. This suggests that new criteria are needed for categorizing trees according to physical state. A measure of the presence and extent of fungal infection is possibly the most direct way to establish if a tree will become a future foraging site for pileated woodpeckers.

Future research on pileated woodpecker foraging ecology would be wise to focus on carpenter ant ecology. Because carpenter ants make up the majority of the pileated woodpecker's diet, it stands to reason that selection criteria of carpenter ants for nest trees should be similar to selection criteria of pileated woodpeckers for foraged trees. Because it is unlikely that pileated woodpeckers locate carpenter ants immediately upon invasion, it follows that foraged trees would be slightly larger, more decomposed, and have higher occurrences of injuries and conks than those selected for invasion by carpenter ants.

In relation to the foraging ecology of pileated woodpeckers further work on tree characteristics is needed. While understanding the preferences of pileated woodpeckers for foraged trees is important in the management of pileated woodpeckers, this researcher would suggest that any future work should concentrate on the characteristics of the trees. Tree species, tree type and stand type should not be ignored but to look at preferences without looking at tree characteristics is to miss the forest among the trees.

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Appendix A

SUMMARY OF STATISTICAL ANALYSES

Kendall's tau-b & Logistic regression

Ordinal variable pairs with Kendall's tau-b correlations of greater than 0.8 (>64% of variance shared) were considered too closely related to be meaningfully combined for further analysis regarding variable interaction. That is, these variables were considered indistinguishable for the purposes of this analysis. Variables sharing less than 64% of variance were used to create interaction variables and entered into a logistic regression using the forward stepwise selection procedure.

Variables were combined by multiplying the values in order to create a new variable for each combination. For example, interaction variable values for DBH by Decay (IVDBHxDecay) were calculated by multiplying the DBH (cm) of each tree by its value for the Decay (0-3) variable. This was done for the following 18 variable combinations:

Using SPSS, the forward stepwise selection procedure was used to build the regression model. The Likelihood-Ratio Test was used as the criterion for determining variables to be removed. Conservative significance levels were used to reduce the influence of the large sample size (3300 > n > 2800 for all analyses). Entry and removal probabilities for each step of the stepwise procedure were set at 0.01 and 0.05, respectively (Hosmer 1989). It was hypothesized that individual tree characteristics

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would be the primary influence on foraging site selection. The null hypothesis was that coefficients for tree characteristic interaction variables were as likely to be zero as coefficients including species indicator variables. If the subgroup of six individual tree characteristic interaction variables entered the model first, and no further variables from the species indicator subset satisfied the criteria for inclusion in the model, the null hypothesis would be rejected.

Foraged trees vs. Non-foraged trees:

Contingency table analyses were used to determine whether the frequency of foraging was independent of frequency of decay class, of injury, and of conk. Student's t-test was used to compare average dbh of foraged to non-foraged trees.

Mixed plots vs. Deciduous plots:

The χ_c^2 goodness-of-fit test was used to compare proportion of trees foraged in mixed plots to proportion of trees foraged in deciduous plots. Student's t-test was used to compare average dbh of foraged trees in mixed plots to that in deciduous plots. Contingency table analyses were used to determine whether frequency of stand type was independent of frequency of decay class, of injury, and of conk.

Coniferous trees vs. Deciduous trees:

The χ_c^2 goodness-of-fit test was used to compare the proportion of foraged coniferous trees to the proportion of foraged deciduous trees. Student's t-test was used to compare dbhs of coniferous and deciduous trees. Student's t-test was also used to compare canopy height and canopy cover at foraged coniferous and deciduous trees and tree/snag height of foraged coniferous and deciduous trees. Contingency table analyses

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were used to determine whether frequency of tree type was independent of frequency of decay class, of injury, and of conk.

Tree species vs. Tree species:

Contingency table analysis was used to determine if frequency of foraging was independent of frequency of tree species. Pair-wise comparisons between proportions of foraged tree species were made for each individual tree species using the Dunnett test statistic (i.e., the species being compared to all others was treated as the control, Zar 1999). Mean dbhs of significantly different groups (i.e., tree species that were significantly different according to the Dunnett test statistic) were compared with student's t-test. Contingency table analyses were used to determine whether the frequency of tree species was independent of the frequency of decay class, of injury, and of conk.

Mixed plots:

In mixed plots, deciduous and coniferous species were analyzed for foraging selection under conditions of their equal availability.

Foraged trees vs. Non-foraged trees:

Contingency table analyses were used to determine whether frequency of foraging was independent of frequency of decay class, of injury, and of conk.

Coniferous trees vs. Deciduous trees:

Proportions of foraged deciduous and foraged coniferous trees were compared using χ_c^2 goodness-of-fit test. Student's t-test was used to compare mean dbhs of deciduous and coniferous trees. Contingency table analyses were used to determine whether frequency of tree type was independent of frequency of decay class, of injury, and of conk.

Tree species vs. Tree species:

A contingency table analysis was used to determine if frequency of foraging was independent of frequency of tree species. Pair-wise comparisons between proportions of foraged tree species were made for each individual tree species using the Dunnett test statistic (i.e., the species being compared to all others was treated as the control, Zar 1999). Mean dbhs of significantly different groups were compared with student's t-test. Contingency table analyses were used to determine whether frequency of tree species was independent of frequency of decay class, of injury, and of conk.

APPENDIX B:

TABLES AND FIGURES CITED IN TEXT.

Table 1. Kendall's tau-b values and % variance shared for interaction variable combinations of tree characteristic variables and of species by tree characteristic variables.

Variable Pair	Kendall's tau-b	% shared variance
Conk * Decay	0.523	27.04
Injury * Decay	0.500	25.00
Injury * Conk	0.421	17.72
Yellow Birch * Conk	0.270	7.30
Yellow Birch * Injury	0.201	4.04
Aspen * Conk	0.176	3.10
Aspen * Injury	0.162	2.62
Yellow Birch * Decay	0.158	2.50
Eastern Hemlock * Decay	-0.141	1.99
Aspen * Decay	0.135	1.82
Eastern Hemlock * Injury	-0.111	1.23
Eastern Hemlock * Conk	-0.089	0.79

Table 2: Interaction variable combinations for individual tree characteristic (ITC) variables and interaction variable combinations for species by characteristic (S-by-C) for aspens, Yellow Birch, and Eastern Hemlock used in logistic regression model.

ITC	S-by-C
Conk by Decay	Aspen by Conk
Injury by Decay	Aspen by Decay
DBH by Decay	Aspen by DBH
Injury by Conk	Aspen by Injury
Injury by DBH	Yellow Birch by Conk
Conk by DBH	Yellow Birch by Decay
	Yellow Birch by DBH
	Yellow Birch by Injury
	Eastern Hemlock by Conk
	Eastern Hemlock by Decay
	Eastern Hemlock by DBH
	Eastern Hemlock by Injury

						Deca	Decay class			
Foraging		Live	,e	Decl	Declining	Dead	ad	Loos	Loose Bark	Decomposed
heart	Observed	2747		124		100	11 30	142	0 63	41
AUSCIIL	Expected	2656.8		131		139.7	11.40	184.1	<u>co.c</u>	42.4
Jungton	Observed	10	01 20	12	10.30	45	V 200	49	156 27	С
rresellt	Expected	100.2	07.10	4.9	10.29	5.3	7.1.67	6.9	10.007	1.6

Table 3. Frequency of foraging among trees in 5 decay classes (see text for definition of decay classes). Bold

Table 4. Frequency of foraging in injured and uninjured
trees. Bold underlined numbers represent statistically
significant post-hoc chi-square test results.

			Inju	ry	
Foraging		Abs	sent	Pr	esent
Absent	Observed	2659		495	13.56
Absent	Expected	2570		584	13.30
Present	Observed	8	81.66	111	260 1
rresent	Expected	97	<u>01.00</u>	22	<u>360.1</u>
d.f. = 1, chi-se	quare $=$ 457.50	0, P < 0.0	01		

Table 5. Frequency of foraging in trees with conks and without conks. Bold underlined numbers represent statistically significant post-hoc chi-square test results.

			Con	k	
Foraging		Abs	sent	Pr	esent
Absent	Observed	3041		113	22.96
Absent	Expected	2977.3		177	<u>22.90</u>
Present	Observed	43	38.03	70	644 1
Fresent	Expected	106.7	<u>30.03</u>	6.3	044.1
d.f. = 1, chi-so	quare = 702.7	8, $P < 0.00$	01		

Plot type	Foraged	Available	Proportion Foraged
Deciduous	40	12,602.60	0.00320
Coniferous	28	6,641.76	0.00420
Zc = 1.03			

Table 6: Number of foraged and available trees in 12deciduous and 10 mixed plots.

					Decay class	class	
Plot type		Live	0	Declining	Dead	Dead Loose Bark	Decomposed
Docidinana	observed	1515		06	75	114	16
Decianons	expected	1524.6	4.44	72.5	80.2	105.6	24.3
	observed	1242		46	70	77	28
MIXEN	expected	1232.4		60.8	64.8	85.4	19.7

Table 7. Frequency of trees in deciduous plots and mixed plot in 5 decay classes. Bold underlined

		Inj	jury
Plot type		Absent	Present
Deciduous	observed	1490	319
Declauous	expected	1474.5	334.5
Miwod	observed	1177	286
Mixed	expected	1192.5	270.5
d.f. = 1, chi-sq	uare $= 1.97, 0$	0.10 < P < 0	.25

Table 8: Frequency of trees in deciduous and mixed plots with and without injuries.

Table 9: Frequency of trees in deciduous and mixed plots with and without conks.

		Co	onk
Plot type		Absent	Present
Deciduous	observed	1711	95
Declauous	expected	1705.4	100.6
Miwad	observed	1373	87
Mixed	expected	1378.6	81.4
d.f. = 1, chi-squ	uare = 0.75 0.	25 < P < 0.	50

Table 10: Number of foraged and available deciduous and coniferous trees in 12 deciduous and 10 mixed plots.

			Proportion
Tree type	Foraged	Available	Foraged
Deciduous	57	11,306.73	0.00504
Coniferous	11	9,147.20	0.00120
Zc = 4.62			

					Decay class	SS		
Tree Type		Live	Declining	ng	Dead	Loose	Loose Bark	Decomposed
Decidinance	Observed	1890		96	116	165	6 27	27
Suburgen	Expected	1953.4		0.20	102.7	135.3	70.0	31.2
Conifornation	Observed	867	15	200	29	26	15 02	17
Subterous	Expected	803.6	-	07.01	42.3	55.7	CO.CI	12.8

Bold underlined numbers represent	
Table 11. Frequency of deciduous and coniferous trees in 5 decay classes. Bold underlined numbers represent	statistically significant post-hoc chi-square test results.

Table 12. Frequency of deciduous and coniferous trees with
and without injuries. Bold underlined numbers represent
statistically significant post-hoc chi-square test results.

]	Injury	
Tree Type		Absent	Pre	sent
Deciduous	Observed	1828	491	8.84
Declauous	Expected	1889.6	429.4	0.04
Coniferous	Observed	839	115	21 40
Connerous	Expected	777.4	176.6	<u>21.49</u>
d.f. = 1, chi-squar	re = 37.25 P < 0	0.001		

Table 13. Frequency of deciduous and coniferous trees with and without conks. Bold underlined numbers represent statistically significant post-hoc chi-square test results.

			Conk		
Tree Type		Absent	Pre	sent	
Deciduous	Observed	2145	169	11.98	
Decluuous	Expected	2184.4	129.6	11.70	
Coniformation	Observed	939	14	20.07	
Coniferous	Expected	899.6	53.4	<u>29.07</u>	
d.f. = 1, chi-squar	re = 43.45, P < 6	0.001			

			Species		
		Eastern	I	White	
Foraging	Aspen	Hemlock	White Cedar	Pine	Yellow Birch
A house Observed	30	598	62	8	256
Expected	40.5	582.8	67.4	9.6	281.3
Observed		7 10 11	8	2	36
Fresent Expected 1	<u>1.5</u>	22.2 <u>10.41</u>	2.6 11.22	0.4 0.4	10.7 20.62

Live Declining Dead Bark Decom 9:56 4 5 16 72:90 0 9:56 1.7 1.9 2.5 72:90 0 9 1.7 1.9 2.5 0 0 0 1.7 1.3 21.34 1.8 0.5 0.1 0.6 9 25.1 13.05 26.8 10.53 5 26.01 8.1 1 7 25.1 13.05 26.8 10.53 5 26.01 8.1 81 73 25.7 0 0 9 9 9 1 6 3 0.9 23.7 4 4 0.4 0.4 1.7 3.9 3.9 4 11.50 21 3.0 22.67 31 1 1 11.50 21 3.0 3.1 1 1 1 0 1 1 1 1							Decay Class	lass				
LiveLiveDecliningDeadBarkObserved179.56451672.90Expected35.49.561.71.92.572.90Expected34.51.7931.3420Expected34.51.7931.3420Expected34.51.7931.3420Expected34.51.7209.68.91726.80.5Expected509.68.917713.0526.80.9Observed1488817500Expected1483.473.2780.90Observed501633Expected55.62.772.9780.9Observed70031Expected8.40.40.417Observed19211.50213031Expected245.111.50213031Expected245.112.23111.53							•		\mathbf{L}_{0}	ose		
Observed179.56451672.900Expected 35.4 2.56 1.7 1.9 2.5 72.90 0.6 Observed 277 9 1.7 1.9 2.5 0.6 0.6 Observed 577 8.91 7 1.7 21.34 1.8 0.5 0.1 Observed 577 8.91 7 1.7 21.34 1.8 0.5 0.1 Observed 577 8.91 7 25.1 13.05 56.8 100 0 Observed 1483.4 73.2 78 0.9 6 23.7 Observed 50 1 75 0 9 23.7 Observed 50 1 6 3 4 Expected 55.6 2.7 2.9 4.1 0.9 Observed 7 0 0 31 1 1 Expected 8.4 0.4 0.4 17 0.9 Observed 192 11.50 21 30 22.67 31 1 Observed 192 11.50 21 30 22.67 31 17 0.1 Observed 245.1 11.50 21 30 22.67 31 17 0.1	Species		Liv	e	Decli	ining	Dea	ad	\mathbf{B}_{2}	ırk	Decor	nposed
Expected 35.4 $\overline{2.9}$ 1.7 1.9 2.5 $\overline{2.9}$ 0.6 Observed 27 9 31.34 1.7 1.9 2.5 0.1 0.6 Observed 577 9 31.34 1.8 0.5 0.1 0.6 Observed 577 8.91 7 12.05 10 10.53 6 26.01 6 Expected 509.6 8.91 77 25.1 13.05 26.8 10.53 6 26.01 6 Observed 1488 81 775 00 0.9 23.7 9 Observed 50 1 73.2 78 0.9 23.7 9 Observed 55.6 2.77 2.9 4.1 0.9 23.7 Observed 7 0.4 0.4 0.4 1.7 0.9 Expected 8.4 0.4 0.4 1.7 0.9 Observed 192 11.50 21 30 22.67 31 11 Observed 245.1 12.2 12.9 22.67 31 117 0.1 Observed 245.1 12.2 12.9 22.67 31 117 0.1	Acnone	Observed	17	920	4		5		16	72 00	0	
Observed 27 9 31.34 2 00Expected 34.5 1.7 31.34 1.8 0.5 0.1 Expected 577 8.91 7 1.7 31.34 1.8 0.5 0.1 Observed 577 8.91 7 12.05 10 10.53 6 26.01 6 Expected 509.6 8.1 75 00 9 9 9 Observed 1483.4 73.2 78 0.9 9 9 Observed 50 1 75 0 9 9 Observed 50 1 75 0 9 9 Observed 50 1 75 0 9 23.7 Observed 56 2.7 2.9 4.1 0.9 23.7 Observed 7 0 0 0 31 1 1 Observed 192 11.50 21 30 22.67 31 17 Observed 192 11.50 21 30 22.67 31 17 Observed 192 11.50 21 30 22.67 31 17 Observed 245.1 12.2 12.9 22.67 31 17 Observed 245.1 12.2 12.9 22.67 31 17 Observed 245.1 12.2 30 22.67 31 17	surplier	Expected	35.4	00.0	1.7		1.9		2.5	06.71	0.6	
Expected 34.5 1.7 $\overline{21.04}$ 1.8 0.5 0.1 Observed 577 8.91 7 1.7 10 10.53 6 26.01 6 Observed 509.6 8.91 25.1 13.05 26.8 10.53 5 26.01 6 Observed 1488 81 75 0 9 9 Observed 50 1 73.2 78 0.9 23.7 Observed 50 1 6 3 4 Observed 50 1 6 3 4 Observed 55.6 2.77 2.9 4.1 0.9 Observed 7 0 0 31 1 1 Observed 17 0.4 0.4 0.4 17 0.1 Observed 192 11.50 21 30 22.67 31 17 Observed 245.1 12.2 12.2 12.9 22.67 31 17 Observed 245.1 12.2 12.9 22.67 31 17	Dlools I court	Observed	27		6	12121	7		0		0	
Observed 577 8.91 7 13.05 10 10.53 6 26.01 6 Expected 509.6 8.91 25.1 13.05 26.8 10.53 5 26.01 6 Observed 1488 81 75 0 9 9 Expected 1488 81 75 0 9 Observed 50 1 6 3 4 Observed 50 1 6 3 4 Observed 50 1 6 3 4 Observed 7 0 0 31 1 Expected 8.4 0.4 0.4 0.4 17 0.9 Observed 192 11.50 21 30 22.67 31 1153 17 Expected 245.1 12.2 12.2 12.9 22.67 31 1153 17	DIACK LOCUSI	Expected	34.5		1.7	+C.IC	1.8		0.5		0.1	
Expected 509.6 25.1 1200 26.8 1000 5 2001 8.1 Observed 1488 81 75 0 9 Expected 1483.4 73.2 78 0.9 23.7 Observed 50 1 6 3 4 Observed 50 1 6 3 4 Observed 55.6 2.7 2.9 4.1 0.9 Observed 7 0 0 31 1 Observed 17 0.4 0.4 0.4 17 0.1 Observed 192 11.50 21 30 22.67 31 17 Expected 245.1 12.2 12.9 22.67 31 11.53 3.9 Expected 245.1 12.2 12.9 22.67 31 11.53 3.9	Eactom Homlool	Observed	577	0.01	7	12.05	10	10 52	9	16 M	9	
Observed 1488 81 75 0 9 Expected 1483.4 73.2 78 0.9 23.7 Expected 50 1 6 3 4 Observed 50 1 6 3 4 Expected 55.6 2.7 2.9 4.1 0.9 Observed 7 0 0 31 1 Observed 12 0.4 0.4 0.4 17 0.1 Observed 192 11.50 21 30 22.67 31 11.53 17 Expected 245.1 11.20 12.2 12.9 22.67 31 11.53 3.9	Eastern mennock	Expected	509.6	16.0	25.1	cn.ct	26.8	<u>cc.ut</u>	S	10.02	8.1	
Expected 1483.4 73.2 78 0.9 23.7 Observed 50 1 6 3 4 Observed 55.6 2.7 2.9 4.1 0.9 Observed 7 0 0 31 1 Observed 7 0 0 31 1 Observed 192 11.50 21 30 22.67 31 Expected 245.1 11.50 12.2 12.9 17 0.1	Manlee	Observed	1488		81		75		0		6	0 1 0
Observed 50 1 6 3 4 Expected 55.6 2.7 2.9 4.1 0.9 Expected 55.6 2.7 2.9 4.1 0.9 Observed700 31 1 Expected 8.4 0.4 0.4 0.4 17 0.1 Observed 192 11.50 21 30 22.67 31 11.53 17 Expected 245.1 11.20 12.2 12.9 22.67 31 11.53 3.9	INTERPIES	Expected	1483.4		73.2		78		0.9		23.7	2.14
Expected 55.6 2.7 2.9 4.1 0.9 -1 Observed7003111Expected 8.4 0.4 0.4 17 0.1 Observed 192 11.50 21 30 22.67 31 11.53 17 Expected 245.1 11.50 12.2 12.9 22.67 31 11.53 3.9	Company	Observed	50		1		9		e		4	10.69
Observed 7 0 0 31 1 Expected 8.4 0.4 0.4 17 0.1 Observed 192 11.50 21 30 22.67 31 11.53 17 Expected 245.1 11.20 12.2 12.9 22.67 31 11.53 3.9	soon rdc	Expected	55.6		2.7		2.9		4.1		0.9	10.00
Expected 8.4 0.4 0.4 17 0.1 Observed 192 11.50 21 30 22.67 31 11.53 17 Expected 245.1 11.50 12.2 12.9 22.67 31 11.53 3.9	White Dine	Observed	L		0		0		31		1	0 1 U
Observed 192 21 30 22.67 31 11.53 17 Expected 245.1 11.50 12.2 12.9 22.67 31 11.53 17		Expected	8.4		0.4		0.4		17		0.1	01.0
Expected 245.1 <u>12.2</u> 12.2 12.9 <u>22.01</u> 17 <u>11.02</u> 3.9	Vollom Rinch	Observed	192	11 50	21		30	77 67	31	11 53	17	
		Expected	245.1	00.11	12.2		12.9	10.77	17	CC.11	3.9	

hoc chi-square test results. Only the data for species in which post-hoc chi-square tests showed significant differences are Table 15. Frequency of 7 tree species in 5 decay classes. Bold underlined numbers represent statistically significant post-

showed significant different	nces are reporte	ed.			
			Inju	ıry	
Species		Abs	sent	Pr	esent
Aspens	Observed	24	<u>15.73</u>	17	<u>69.05</u>
Aspens	Expected	38.7	<u>13.75</u>	2.3	09.03
Black Walnut	Observed	2		0	6 40
DIACK Wallut	Expected	1.9	-	0.1	<u>6.40</u>
Balsam Fir	Observed	199		4	11 20
Daisaili Fir	Expected	191.6	-	11.4	<u>11.29</u>
Eastern Hemlock	Observed	597	614	8	27.01
Eastern Hennock	Expected	571.1	<u>6.14</u>	33.9	<u>27.01</u>
₩7-11 D !li	Observed	216	22.24	74	00.02
Yellow Birch	Expected	273.8	<u>22.34</u>	16.2	<u>98.23</u>
d.f. = 15, chi-square = 291	.44, P < 0.001				

Table 16. Frequency of 5 tree species with and without injuries. Bold underlined numbers represent statistically significant post-hoc chi-square test results. Only the data for species in which post-hoc chi-square tests showed significant differences are reported.

Table 17. Frequency of 4 tree species with and without conks. Bold underlined numbers represent statistically significant post-hoc chi-square test results. Only the data for species in which post-hoc chi-square tests showed significant differences are reported.

			Со	nk	
Species		Abs	ent	Pr	esent
Aspens	Observed	11	<u>5.58</u>	31	93.95
Aspens	Expected	34.2	<u>3.30</u>	7.8	<u> </u>
Eastern Hemlock	Observed	548		57	19.78
Laster II Heimock	Expected	493	-	112	17.70
Maples	Observed	1453		307	5.14
wapies	Expected	1434.1	-	326	<u>3.14</u>
Yellow Birch	Observed	165	12.20	127	206.22
	Expected	237.9	12.20	54.1	<u>200.22</u>
d.f. = 15, chi-square = 364	.07, P < 0.001				

			Proportion
	Foraged	Available	Foraged
Deciduous	38	4,939.96	0.00769
Coniferous	17	5,088.73	0.00334
Zc = 4.62			

Table 18. Number of foraged and available deciduous and coniferous trees in mixed plots.

Ichicscill statistically		non-read min	nin-syud	אוצווווכמוון איטאר-ווטל כווו-אין מאול וכאווא.				
					Decay class			
Foraging		Live	e	Declining	Dead	Loos	e Bark	Loose Bark Decomposed
Ahant	Observed	1235		43	53	52	ууу	26
AUDSUIL	Expected	1196.2		44.3	67.4	74.2	10.0	27
Duccont	Observed	7	27 07	б	17 TO TE	25	176.04	2
	Expected	45.8	07.01	1.7	2.6 2.6	2.8	T/0.04	1
d.f. = 4, chi-square =	1000000000000000000000000000000000000	299.04, $P < 0.001$						

es. Bold underlined numbers		
Table 19. Frequency of foraging among trees in mixed plots in 5 decay classes. Bold underlined numbers	represent statistically significant post-hoc chi-square test results.	

Table 20. Frequency of foraging among trees in mixed plots with and without injuries. Bold underlined numbers represent statistically significant post-hoc chi-square test results.

			Inju	ıry	
Foraging		Abs	ent	Pr	resent
Abcont	Observed	1171		238	5 28
Absent	Expected	1132.8		276	<u>5.28</u>
Dresont	Observed	6	22.01	49	125 11
Present	Expected	44.2	<u>33.01</u>	10.8	<u>135.11</u>
d.f. = 1, chi-s	square = 175.0	08, P < 0.0	001		

Table 21. Frequency of foraging among trees in mixed plots with and without conks. Bold underlined numbers represent statistically significant post-hoc chi-square test results.

			Co	nk	
Foraging		Abs	ent	Pr	esent
Absent	Observed	1355		54	11.24
Absent	Expected	1324.1		84.9	11.24
Drocont	Observed	18	10 52	34	208
Present	Expected	48.9	<u>19.53</u>	3.1	<u>308</u>
d.f. = 1, chi-s	square $= 335.0$	66, P < 0.0	001		

					Γ	Decay class			
Tree Type		Li	Live	Decl	Declining	Dead	Loose Ba	ark	Loose Bark Decomposed
Decidinance	Observed	587	17 75	63	969	43	54	77	11
neuron	Expected	619.7	11.40	23	0.2.0	34.9	38.4		14
Coniforning	Observed	655		11	969	27		31	17
contation on s	Expected	622.3		23	0.2.0	35.1	38	10.0	14

Table 22. Frequency of deciduous and coniferous trees in mixed plots in 5 decay classes. Bold underlined represent statistically significant most-had chi-source test results numbers

Table 23. Frequency of deciduous and coniferous trees in mixed plots with and without injuries. Bold underlined numbers represent statistically significant post-hoc chi-square test results.

			Injury	
Tree Type		Absent	Pre	sent
Deciduous	Observed	545	186	12 72
Declauous	Expected	587.7	143.3	<u>12.72</u>
Coniformation	Observed	632	101	12 60
Coniferous	Expected	589.3	143.7	<u>12.69</u>
d.f. = 1, chi-squar	re = 31.60, P < 100	0.001		

Table 24. Frequency of deciduous and coniferous trees in mixed plots with and without conks. Bold underlined numbers represent statistically significant post-hoc chi-square test results.

			Conk	
Tree Type		Absent	Pre	sent
Deciduous	Observed	655	74	20.63
Decluuous	Expected	685.1	43.9	<u>20.05</u>
Coniferous	Observed	718	14	20.54
Connerous	Expected	687.9	44.1	<u>20.54</u>
d.f. = 1, chi-squar	re = 43.79, P < 100	0.001		

statistically s tests showed	statistically significant post-hoc chi-square test results. Only data for species in which post-hoc chi-square tests showed significant differences are reported.	-hoc chi ferences	i-square to s are repo	est results. rted.	Only dat	a for sp	ecies in v	vhich po	ost-hoc	: chi-squ	are
						Species	es				
				Eastern	ern			White	ite		
Foraging		As	Aspen	Hemlock	ock	White	White Cedar	Pine	e	Yellow Birch	Birch
A heavet	Observed	20		503		62		8		131	
AUSCIIL	Expected	24.1		489.9		67.4		9.6		147.3	
Duccont	Observed	5	1060	9	000	8	11 23	0	УY	22	17 F1
rresent	Expected	0.9	10.00	19.1	0.70	2.6	77.11	0.4	†	5.7	10.04
d.f. = 8, chi-s	d.f. = 8, chi-square = 93.82, P < 0.001	P < 0.0	001								

Frequency of foraging among 5 species of trees in mixed plots. Bold underlined numbers represent	lly significant post-hoc chi-square test results. Only data for species in which post-hoc chi-square	ved significant differences are reported.
Table 25. Frequen	statistically signifi	tests showed signi

inces are shown. The Declining Dead Loose Bark Decomposed erved 12 0 0 13 105 3 0	of 6 tree species in mixed plots among 5 decay classes. Bold underlined numbers represent int post-hoc chi-square test results. Only data for species in which post-hoc chi-square tests
showed significant differences a Species Observed Observed	Table 26. Frequency of 6 tree sp statistically significant post-hoc
showed significant differences are shown. Species Live Declir	Table 26. Frequency of 6 tree species in mixed plots among statistically significant post-hoc chi-square test results. On

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y clas	or sp	
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sy of 6 tree species in mixed plots among 5 decay classes. Bold underlined numbers represent	cant post-hoc chi-square test results. Only data for species in which post-hoc chi-square tests	
s amc	ilts. (
l plot	t resu	
mixe	re tes	_
es in 1	-squa	howr
specie	c chi	differences are shown
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uency	nifica	-
Freq	ly sig	d significant
able 26. Free	tatisticall	ved si
Table 20	stati	showe

						Decay	y Class				
Species		Live	e	Declining	ining	De	Dead	Loose	Loose Bark	Decoi	Decomposed
A croas	Observed	12		0		0		13	105 3	0	
SUDUCE	Expected	21.2		0.8		0.8		1.3	CICOT	0.5	
Rolcom Fir	Observed	63		ε		7		10	2 06	9	10.99
Dalsalli L'II	Expected	75.6		2.8		4.3		4.7	02.0	1.7	10.00
Eastern	Observed	483	У	9	202	10	4 0	4	10.1	9	
Hemlock	Expected	432.1	91	16.6	<u> 77.0</u>	24.4	0.0	26.8	1 7.4	9.7	
Monloo	Observed	450		24		26		27		-	())
INTAPICS	Expected	448.2		16.6		25.3		27.8		10.1	7.0
Commond	Observed	42		-		9		4		4	7 65
soon rdc	Expected	48.4		1.8		2.7		ε		1.1	<u>co./</u>
Vallaw Rinch	Observed	101	6 08	10	2 62	17	17 80	14		10	17 30
	Expected	129	00	4.8	0.0.0	7.3	14.07	8		2.9	1/.00
d.f. = 32, chi-square =	e = 258.12, P < 0.001	0.001									

Table 27. Frequency of 3 tree species in mixed plots with and without injuries. Bold underlined numbers represent statistically significant post-hoc chi-square test results. Only data for species in which post-hoc chi-square tests showed significant differences are shown.

			In	jury	
Species		Abs	ent	Pr	esent
Aspens	Observed	6	<u>9.89</u>	19	40.57
Aspens	Expected	20.1	9.09	4.9	40.37
Eastern	Observed	463	7 07	46	295.35
Hemlock	Expected	409.2	<u>7.07</u>	99.8	<u> </u>
Yellow Birch	Observed	83	12	70	52.22
I CHOW DIFCH	Expected	123	<u>13</u>	30	<u>53.33</u>
d.f. = 8, chi-squa	re = 168.05, 1	P < 0.00	1		

Table 28. Frequency of 3 tree species in mixed plots with and without conk. Bold underlined numbers represent statistically significant post-hoc chi-square test results. Only data for species in which post-hoc chi-square tests showed significant differences are shown.

			С	onk	
Species		Abs	ent	Pr	esent
Aspons	Observed	14		11	60.17
Aspens	Expected	23.5	-	1.5	00.17
Eastern	Observed	501		8	16.79
Hemlock	Expected	478.3	-	30.7	10.79
Vallaw Dinah	Observed	113	6 22	39	06 52
Yellow Birch	Expected	142.8	<u>6.22</u>	9.2	<u>96.53</u>
d.f. = 8, chi-squa	re = 194.59,	P < 0.00	1		

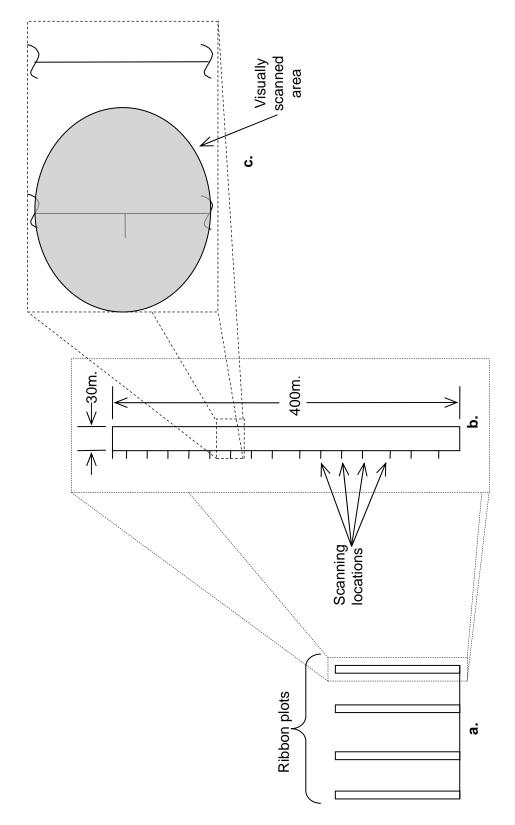


Figure 1: Diagram of a. ribbon plot distribution design, b. individual ribbon plot, demonstrating location of 25m interval scanning locations and c. individual scanning location, approximating area covered in 360° arc scan.

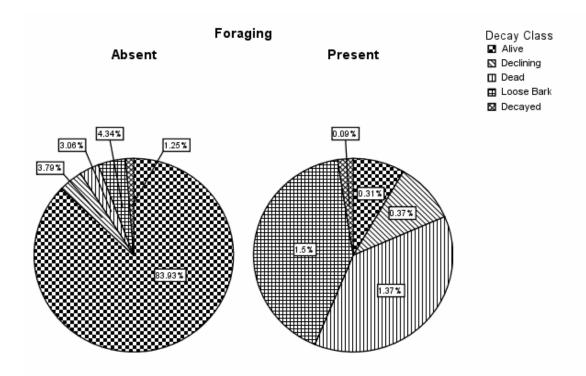


Figure 2: Percents of decay classes for non-foraged and foraged trees in Dukes Experimental Forest.

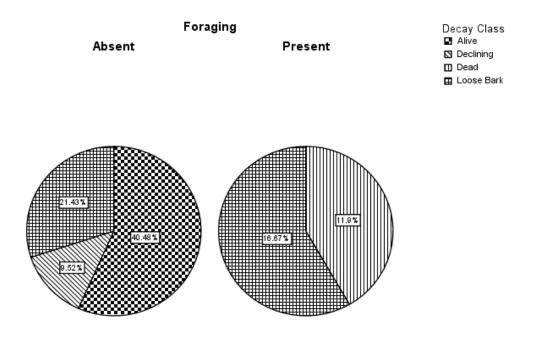


Figure 3: Percents of decay classes for non-foraged and foraged aspen trees in Dukes Experimental Forest.

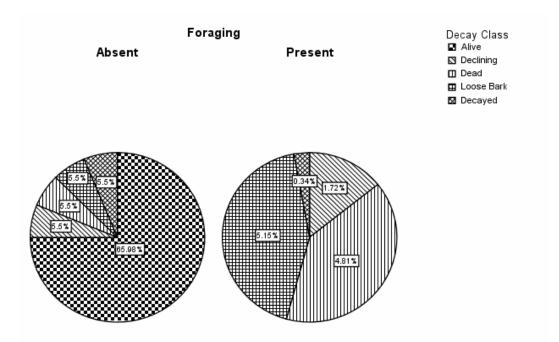


Figure 4: Percents of decay classes for non-foraged and foraged yellow birch trees in Dukes Experimental Forest.

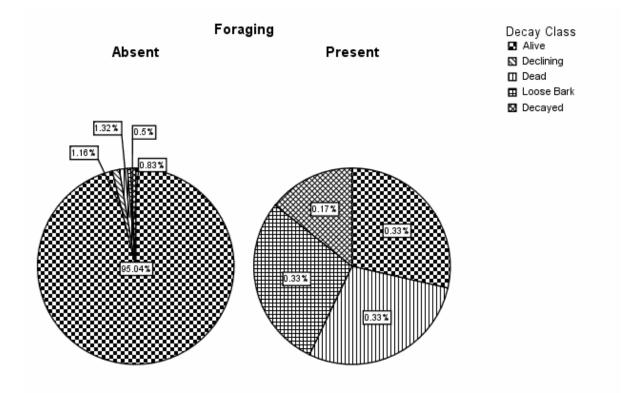


Figure 5: Percents of decay classes for non-foraged and foraged eastern hemlock trees in Dukes Experimental Forest.

APPENDIX C

SAMPLE FORAGING DATA SHEET

FORAGING TREE RECORD

Plot						
Tree #						
Date						
UTM						
Species						
DBH						
Tree/snag height @m°						
Max foraging height @m°						
Decay class:Live—Declining—Dead—Loose Bark—No Bark—	-Decomposed					
Injury (fire, lightning, frost crack, forked top, broken top) presen	tabsent					
Conkpresentabsent						
Canopy height @m°						
Canopy cover: (count of $\frac{1}{4}$ squares not filled with canopy)						
N, E, S, W AVE	RAGE					
Foraging age						

APPENDIX D:

SAMPLE HABITAT DATA SHEET

Plot			HABITAT PLOT RECORD					
Bloc	ck #							
UTN	Л							
Cano	opy Heigh	t C:_	N	: E_	:	S:_	W	_:
Cano	opy Cover	• C	_ N	E	S	W		
	TREE #	SPECIES	DBH	HEIGHT Dist : Deg	DECAY	INJURY	CONK	
1				:				
2				:				
3				:				
4				:				
5				:				
6				:				
7				:				
8				:				
9 10				:				
11				•				
12				•				
13				:				
14				:				
15				:				
16				:				
17				:				
18				:				
19				:				
20				:				
21				:				
22				:				