Wilson Bull., 106(2), 1994, pp. 242–257

SNAG CONDITION AND WOODPECKER FORAGING ECOLOGY IN A BOTTOMLAND HARDWOOD FOREST

RICHARD N. CONNER,[1] STANLEY D. JONES,[2] AND GRETCHEN D. JONES[2]

ABSTRACT.—We studied woodpecker foraging behavior, snag quality, and surrounding habitat in a bottomland hardwood forest in the Stephen F. Austin Experimental Forest from December 1984 through November 1986. The amount and location of woodpecker foraging excavations indicated that woodpeckers excavated mainly at the well-decayed tops and bases of snags. Woodpeckers preferred to forage on oaks (*Quercus* spp.) (snags and live trees) whereas blue beech (*Carpinus caroliniana*) and red maple (*Acer rubrum*) were used less than expected. Snags used for foraging excavations were generally 3–10 m in height, mainly located in older stands, and lacked bark at excavated foraging sites. In the bottomland habitat, Downy Woodpeckers (*Picoides pubescens*) foraged on smaller diameter substrates and used more tree species than other woodpecker species. Pileated Woodpeckers (*Dryocopus pileatus*) foraged either near the ground or in the upper zones of trees. Red-bellied Woodpeckers (*Melanerpes carolinus*) used a restricted range of tree diameters and locations in trees. Red-headed Woodpeckers (*M. erythrocephalus*) used the greatest diversity of foraging methods and foraged on the largest range of tree diameters. *Received 27 April 1993, accepted 12 Aug. 1993.*

Many woodpecker species depend on snags (standing dead trees) for foraging sites (Kisiel 1972, Conner 1980, Mannan et al. 1980, Brawn et al. 1982, Raphael and White 1984, Morrison and With 1987). Until recently (Rosenberg et al. 1988), little attention has been focused on the characteristics of snags associated with high quality foraging. Because characteristics of snags may vary regionally, it is important to examine snag use relative to condition in a variety of forest types. In addition, the value of snags as nesting and roosting sites for woodpeckers and other cavity nesters is well known (Conner 1978, Evans and Conner 1979, Thomas et al. 1979, Raphael and White 1984).

Bottomland hardwood forests are dwindling and typically have relatively abundant woodpecker populations. More than 63% of the original southeastern bottomland hardwood forests have been lost, and the current rate of loss per decade in eastern Texas is about 14% (USFWS 1984). Knowledge of the sizes, species, bark condition, and decay conditions of

[1] Wildlife Habitat and Silviculture Laboratory (maintained in cooperation with the College of Forestry, Stephen F. Austin State Univ.), Southern Forest Experiment Station, USDA Forest Service, Nacogdoches, Texas 75962.

[2] Dept. of Biology, Stephen F. Austin State Univ., Nacogdoches, Texas 75962. (Present address SDJ: Department of Rangeland Ecology and Management, S. M. Tracy Herbarium, Texas A&M Univ., College Station, Texas 77843-2126. Present address GDJ: Dept. of Biology, Texas A&M Univ., College Station, Texas 77843-3258).

snags and trees that are used by woodpeckers is important for the provision of such habitat in this critical habitat type. Determination of forest structure that is conducive to snag formation could aid management of such habitat.

We examined woodpecker foraging behavior, snag size and condition, and surface area of foraging excavations on snags to evaluate snag quality and woodpecker foraging ecology in bottomland hardwood forests. Forest stand structure around snags was evaluated to determine what environmental conditions are associated with snags that have high use by foraging woodpeckers.

STUDY AREA AND METHODS

The study area (28.7 ha) was centrally located in a bottomland hardwood forest on the floodplain of the Angelina River in the Stephen F. Austin Experimental Forest (31°29′N, 94°47′W) in southern Nacogdoches County, Texas. Of 1038 ha of forested bottomland habitat in the experimental forest, approximately 650 ha are in the flood plain. The study area contained 66.7 snags/ha (10.2% of vertical stems) and 585 live hardwoods/ha (89.8%) (Jones 1987). The last timber harvest occurred on the experimental forest in 1920 when some high value trees were logged selectively. The dominant trees by percentage of live hardwoods were sweetgum (*Liquidambar styraciflua*), oak species [including water oak (*Quercus nigra*), overcup oak (*Q. lyrata*), Nuttall's oak (*Q. nuttallii*), willow oak (*Q. phellos*), swamp chestnut oak (*Q. michauxii*)], blue beech (*Carpinus caroliniana*), and black gum (*Nyssa sylvatica*). The average diameter at breast height (DBH) of all trees (including snags) with a DBH of 10 cm or more was 23.4 cm; the average height of these trees was 33.2 m (Jones 1987). A mid-story layer of blue beech, eastern hop-hornbeam (*Ostrya virginiana*), water elm (*Planera aquatica*), and hollies (*Ilex* spp.) was present. The soils of the bottomland are of the Manatachie series (U.S. Soil Conservation Service 1980) and are poorly drained and highly acidic. The water table is near the surface, and water depths of up to 1.5 m can persist for up to two months.

We collected data on snags, live trees, surrounding habitat, and woodpecker foraging behavior from December 1984 through September 1986.

Vegetation and study tree measurements.—Forty-three snags, seven live trees with dead portions, and 10 live trees were selected randomly (using a spinning pointer at systematically selected fixed points) from their respective populations during January 1985 to provide a variety of tree species and substrate conditions ranging from well-decayed to minimal or no decay. Selected trees (study trees) were greater than 12 cm DBH and far enough apart (>25 m) so that plots did not overlap. Snag species (based on bark characteristics), height (clinometer), and DBH (diameter tape) were measured while trees were standing. We measured tree density, relative density, dominance, relative dominance, frequency, relative frequency, and importance value (see Curtis and McIntosh 1951) within a 0.04 ha ($1/25$ ha) circular plot (11.3 m radius) around each study tree (Conner 1980). We calculated average DBH and basal area of all live hardwoods and snags (≥12 cm DBH) from diameter measurements (Table 1). We divided trees into three DBH size classes (class one = 10–18 cm; class two = 19–38 cm; and class three = >38 cm) to reflect sapling, pole, and sawtimber-sized trees.

In June 1986, we felled 52 of the 60 study trees (8 were deemed too dangerous to fell), measured, and divided them into four equal-length bole zones: lower, lower middle, upper middle, and upper. We measured the percentage of residual bark attached to each snag within each height zone (e.g., percentage of residual bark on the lower zone) on the exposed

TABLE 1

CHARACTERISTICS OF ENVIRONMENTAL VARIABLES MEASURED IN 0.04 HA PLOTS CENTERED ON 60 STUDY TREES IN A BOTTOMLAND HARDWOOD FOREST IN EASTERN TEXAS

Variable	Mean	SD	Range
Dominant vegetation height (m)	33.2	8.4	18.9–50.3
Basal area of live hardwoods (m^2 per 0.04 ha)	1.4	0.7	0.1–3.0
Basal area of snags (m^2 per 0.04 ha)	0.3	0.3	0.0–1.4
Live hardwoods per 0.04 ha plot	23.4	9.8	8.0–47.0
Snags per 0.04 ha plot	2.7	1.6	1.0–7.0
Logs per 0.04 ha plot	4.7	3.1	0.0–14.0
Average diameter at breast height (cm)	24.1	4.3	16.5–37.7
Class one: number of trees (10–18 cm) per 0.04 ha plot	14.4	7.1	4.0–38.0
Class two: number of trees (19–38 cm) 0.04 ha plot	7.4	4.2	0.0–23.0
Class three: number of trees (>38 cm) per 0.04 ha plot	4.3	1.9	0.0–8.0
Number of tree species per 0.04 ha plot	7.1	2.0	3.0–11.0
Distance to water (m) (sloughs or creeks)	33.4	26.0	0.0–100.0

portion of the bole in each zone and extrapolated for the entire circumference. Because some bark was dislodged during felling, darkened, moist areas of the bole were measured as if they still were covered by bark. An average of the percentages of residual bark for each zone yielded the percentage for the entire study tree.

Pilodyn® measurements of sapwood hardness.—We measured tree hardness within each of the four height zones. A two-joule Proceq pilodyn® was used to measure wood hardness (Sprague et al. 1983). A pilodyn® fires a precision spring-loaded steel pin into the sapwood with a constant force measuring penetration depth (mm). If present, we removed bark at measurement sites to allow direct access to the sapwood. Three measurements per height zone were taken and averaged. We made measurements within 3 cm of woodpecker foraging sites when excavation holes were present. If woodpecker foraging sites were not present, we made measurements in the middle portion of each height zone at three equidistant positions around the circumference of the bole. Penetration depth is inversely related to wood hardness.

Specific gravity determinations of study tree sapwood.—As a relative indicator of extent of decay, we extracted a wood sample (approx. 1 × 3 cm) from each of the four height zones of each felled study tree to determine the sapwood's specific gravity. Decay by basidiomycetes in trees oxidizes lignin and cellulose, softens the wood, and replaces structural wood with air (Cartwright and Findlay 1958, Overholts 1977). Thus, for a given tree species, lower specific gravity values indicate more fungal decay. We extracted wood samples from sites within or adjacent to foraging sites to measure more precisely specific gravity of wood (decay extent) where woodpeckers had foraged. If woodpecker foraging sites were not present, we extracted wood samples in the middle portion of each height zone at three equidistant positions around the circumference of the bole. Specific gravity was measured and calculated

using the two formulas described by Smith (1954) and values averaged because results varied by as much as 0.08 g.

Measurement of woodpecker foraging sign and arthropods on study trees.—We measured the surface area of woodpecker foraging sign (pecking, scaling, and excavation, later converted to percentage of the bole with woodpecker foraging sign) on the boles of felled study trees by height zone. Five ellipses representing common excavation sizes observed on snags (1, 7, 50, 72, and 97 cm^2) were drawn on cardboard in the field and measured with a Licor® LI-3000 electronic portable area meter in the lab. We measured/estimated the surface area of all visible foraging sites by comparing the nearest ellipse size to the foraged area for each of the four bole height zones. If the foraged area lay between sizes or was larger than the largest ellipse, an estimation was made. Because approximately 25% of the tree's surface was on the ground, and not visible, the final summation for each height zone was made by dividing the measured amount by three and multiplying the quotient by four. The total surface area of each height zone was calculated using height and diameter measurements in order to determine the percentage of the bole's surface excavated by woodpeckers. We did not include excavations that clearly appeared to be cavity starts in our measurements of foraging sign. Use of only signs of pecking, scaling, and excavation obviously misses indications of woodpecker foraging that involved peer-and-poke foraging and other superficial gleaning techniques.

We assumed that foraging sign indicated the presence of arthropod prey because nearly all excavation sites penetrated beetle, ant, or termite galleries (live arthropods were regularly observed) that were hidden within the bole, thus, indicating the quality of study tree height zones as foraging sites. Variable time periods elapsed between when woodpeckers foraged on study trees and our measurement of foraging sign. However, the relative differences of foraging sign among height zones on individual trees should accurately reflect woodpecker use of the different zones. We did not determine the species of woodpecker that actually made the excavations on study trees.

To test the assumption that foraging sign indicated the presence of arthropod prey, we removed two blocks of wood (approximately 20 × 20 × 15 cm) from the upper and lower height zones on each study tree. We removed these wood samples from portions of the snags where woodpecker foraging sign was absent. Arthropods that emerged and those obtained during subsequent dissection of the blocks of wood were identified to order and counted (Borror and White 1970). Arthropod samples were oven dried at 85°C to constant weight.

Behavioral observations on foraging woodpeckers.—We observed foraging behavior on initial contact with Downy (*Picoides pubescens*) (N = 189), Pileated (*Dryocopus pileatus*) (N = 100), Red-bellied (*Melanerpes carolinus*) (N = 111), and Red-headed (*M. erythrocephalus*) (N = 250) woodpeckers throughout the year from December 1984 to September 1986. Although Hairy Woodpeckers (*Picoides villosus*), Yellow-bellied Sapsuckers (*Sphyrapicus varius*), and Northern Flickers (*Colaptes auratus*) were present, we collected insufficient data on these species for inclusion. We timed the duration of foraging behaviors, as well as the behavior at the initial time of contact with a woodpecker with a stop watch, and recorded the information on a cassette recorder. Visibility often was difficult, especially during the summer months when a dense canopy cover reduced light and a thick mid-story and sometimes dense understory obscured observations of foraging woodpeckers. Typically, durations of behavioral observations were very short due to foliage obscuring woodpeckers and bird movements. This was a particular problem with Pileated Woodpeckers because of their wariness.

We divided foraging methods into six behaviors (revised from Conner 1981) and noted foraging location within the tree. Peer-and-poke foraging was limited to surface gleaning.

Scaling involved active removal of bark in search of food items. Excavating was differentiated from pecking when the cambial layer was penetrated. Hawking and foraging on logs were also noted. We measured the locations of foraging woodpeckers on trees (trunk, branch, twig) and conditions (live, dead part of live, snag) of the foraging substrates. Branches were lateral stems larger than 2 cm in diameter, whereas twigs were stems <2 cm in diameter.

Analyses.—We used Chi-square analyses and Bonferroni's test (Miller 1981, Byers et al. 1984) to evaluate woodpecker foraging preference among tree species. A wide range of substrate conditions (snags to live trees) was selected to permit examination of correlative relationships, or discriminant analysis if low and high use sites tended to be bimodal. A frequency histogram using the amount of woodpecker foraging sign revealed a bimodal distribution with a midpoint equally dividing the sample of study trees. Snags (dead trees and live trees with dead portions) with foraging sign on >6% of the total surface area were grouped as "high use" foraging sites (N = 25), whereas those with ≤6% were considered "low use" foraging sites (N = 25). We used Mann-Whitney *U*-tests and *t*-tests to compare the surrounding habitats and characteristics of high and low use snags. We tested for heterogeneity of variances between groups during *t*-tests and selected appropriate significance probabilities based on variance equality (SAS 1988).

We also used two-group discriminant analysis to compare high and low use snags. Box's *M* test indicated that group covariance matrices were homogeneous ($P = 0.35$), a necessary assumption for discriminant analysis. Prior probabilities of classification for the discriminant analysis were set equivalent to sample sizes.

We used one-way analysis of variance (ANOVA, $P < 0.05$) to examine woodpecker foraging behaviors, and Chi-square and Bonferroni's test (Byers et al. 1984) to examine the foraging preferences among the woodpeckers for particular tree species. We used correlation analysis to examine relationships among woodpecker foraging sign, arthropod biomass, snag hardness, and specific gravity.

RESULTS

Vegetative characteristics of the study area.—Characteristics of study trees and surrounding habitat varied extensively, providing a range of sites for woodpecker foraging (Tables 1 and 2). Sweetgum and oaks were the most frequent species in the plots (Table 3). We were unable to identify the species of 15% of the snags. Only black gum snags occurred at a higher frequency than its live hardwood counterpart, indicating either a higher snag formation rate or a slower decay rate than other tree species.

A total of 1404 live hardwoods (35.4 m^2/ha basal area), 1 loblolly pine (*Pinus taeda*), and 160 snags (6.7 m^2/ha) comprising 20 tree species were present within the 60 study plots (Table 1). Snags comprised 10.2% of all trees in the study site. Based on importance values, the dominant overstory species (excluding snags) were sweetgum, black gum, water oak, and over-cup oak. The upper canopy layer was dense and uniform except where fallen trees, sloughs, and creek channels existed. Blue beech, red maple (*Acer rubrum*), and species with small DBH's such as deciduous holly (*Ilex decidua*) comprised the midstory. Live trees between 12 and 18 cm diameter (811 trees) comprised 58% of the study

TABLE 2

CHARACTERISTICS OF THE 60 STUDY TREES IN A BOTTOMLAND HARDWOOD FOREST ON THE STEPHEN F. AUSTIN EXPERIMENTAL FOREST

Variable	Mean	SD	Range
Study tree height (m)	9.3	5.4	2.4–25.9
Diameter at breast height (cm)	37.2	17.9	12.0–83.0
Wood hardness lower (mm)	29.3	12.4	7.0–45.0
Wood hardness lower middle (mm)	25.0	13.4	6.0–45.0
Wood hardness upper middle (mm)	28.2	13.4	6.0–45.0
Wood hardness upper (mm)	32.3	12.8	3.0–45.0
Wood hardness of total tree (mm)	28.7	11.6	3.0–45.0
Percentage of bark lower zone	61.1	39.3	0.0–100.0
Percentage of bark lower middle zone	66.0	35.2	0.0–100.0
Percentage of bark upper middle zone	63.1	37.6	0.0–100.0
Percentage of bark upper zone	34.6	37.4	0.0–100.0
Percentage of bark total tree	56.4	29.1	0.0–100.0
Specific gravity lower zone	0.3	0.1	0.1–0.6
Specific gravity lower middle zone	0.3	0.1	0.1–0.7
Specific gravity upper middle zone	0.3	0.1	0.1–0.7
Specific gravity upper zone	0.3	0.1	0.1–0.6
Specific gravity total tree	0.3	0.1	0.1–0.7

area, trees 19 to 38 cm (382 trees) 27%, and trees >38 cm (212 trees) 15%. Most of the sweetgum trees were in the smallest size class, while black gums were mainly >38 cm DBH. No blue beech was recorded larger than 18 cm.

TABLE 3

FREQUENCIES OF LIVE HARDWOODS AND SNAGS, AND PERCENTAGE OF TREE SURFACE AREA WITH WOODPECKER FORAGING SIGN IN A BOTTOMLAND HARDWOOD FOREST

Tree species	Frequency of live hardwoods (%) N = 1404	Frequency of snags (%) N = 160	Amount of woodpecker foraging sign (%)
Sweetgum	31.6	25.5	29.8
Oak species	29.8	24.9	42.4[a]
Blue beech	12.0	8.1	0.7[b]
Black gum	10.7	16.2	22.9
Red maple	8.6	3.1	1.6[b]
Unidentified	0	15.5	
Others	7.3	6.8	2.7[b]

[a] Bonferroni's test, $P < 0.05$, foraging intensity significantly greater than expected.
[b] Bonferroni's test, $P < 0.05$, foraging intensity significantly less than expected.

TABLE 4

COMPARISON OF SNAGS (N = 50) WITH EXTENSIVE FORAGING SIGN (>6%) WITH SNAGS USED LESS FREQUENTLY (≤6%) USING A TWO-TAILED *T*-TEST

Snag variable	Foraging sign >6%	Foraging sign ≤6%	*t*	*P*
Snag height (m)	7.6 (25)	10.8 (25)	2.05	0.046
Snag DBH (cm)	37.9 (25)	36.5 (25)	0.28	0.785
Snag hardness lower (mm)	34.8 (23)	23.5 (22)	3.37	0.002
Snag hardness lower middle (mm)	30.0 (23)	19.8 (22)	2.72	0.010
Snag hardness upper middle (mm)	34.1 (23)	22.1 (22)	3.33	0.002
Snag hardness upper (mm)	37.5 (23)	26.8 (22)	3.06	0.004
Percent bark lower (%)	46.6 (23)	76.3 (22)	2.70	0.010
Percentage bark lower middle (%)	53.5 (23)	81.0 (22)	2.82	0.007
Percentage bark upper middle (%)	55.2 (23)	71.4 (22)	1.46	0.151
Percentage bark upper (%)	26.1 (23)	43.4 (22)	1.58	0.122
Specific gravity lower	0.32 (23)	0.31 (22)	0.17	0.864
Specific gravity lower middle	0.31 (23)	0.35 (22)	1.33	0.191
Specific gravity upper middle	0.26 (23)	0.31 (22)	1.55	0.130
Specific gravity upper	0.27 (23)	0.31 (22)	0.90	0.374

Discriminant analysis ($P < 0.032$, overall classification success was 72%) using environmental variables was calculated to compare high use snags (N = 25) with low use snags (N = 25). Snags exhibiting high use by foraging woodpeckers were located in habitat that had a higher basal area of live hardwoods ($r = 0.76$, $P < 0.01$, correlation of original variable with the discriminant function), larger average diameter trees ($r = 0.66$, $P < 0.01$), and more trees >38 cm ($r = 0.51$, $P < 0.01$) than habitat with low use snags.

Woodpecker foraging sign on study trees and arthropod biomass.—Woodpeckers foraged on certain tree species more than others ($\chi^2 = 152.3$, $P < 0.001$); oaks were most preferred (Table 3). Woodpecker foraging sign on sweetgum approximated its frequency of occurrence, whereas blue beech and red maples were used less than expected. The pilodyn® typically penetrated live trees only 9–15 mm. Higher pilodyn® values indicate greater decay because of deeper penetration of the striker pin. Lower values of specific gravity indicate greater decay. Trees with signs of high foraging use consistently yielded average pilodyn® readings of over 30 mm, indicating a softer, more decayed condition (Table 4). Specific gravity measurements of all tree species combined were highly correlated ($r = -0.768$, $P < 0.001$) with pilodyn® measures of hardness (Table 5). Short and soft snags had the greatest amount of foraging sign (Table 4). Snags with extensive foraging sign were also in more advanced

TABLE 5

PEARSON CORRELATIONS OF PERCENTAGE OF SNAG SURFACE AREA WITH WOODPECKER FORAGING SIGN AND SNAG QUALITY VARIABLES

Snag quality variables	Woodpecker foraging sign	Snag height	Snag DBH	Snag hardness	Percent bark
Snag height	−0.358[a]				
Snag DBH	−0.140	0.459[a]			
Snag hardness	0.473[a]	0.005	0.432[a]		
Percent bark	−0.191	0.212	0.316	−0.109	
Specific gravity	−0.376[a]	−0.081	−0.452[a]	−0.768[a]	−0.142

[a] $P < 0.01$.

stages of decay (Mann-Whitney, $U = 145.5$, $P < 0.001$; see snag hardness, Table 4).

Woodpecker foraging sign was more prevalent in the highest ($\bar{x} = 3.3\% \pm 3.6$ (SD), range = 0 to 14.5) and lowest ($\bar{x} = 3.5\% \pm 4.2$, range = 0 to 57.9) height zones of the snags. Evidence of woodpecker foraging was less abundant in the upper middle ($\bar{x} = 1.8\% \pm 2.6$, range = 0 to 13.4) and lower middle ($\bar{x} = 2.1\% \pm 3.0$, range = 0–13.4) zones. The location of woodpecker foraging sign (above), percentage of residual bark, and snag hardness at the four standardized height zones (Table 4) collectively indicate that woodpeckers foraged most often on the well-decayed, softer portions of snags (Fig. 1). The percentage of residual bark on snags was inversely related to the amount of woodpecker foraging sign; and residual bark was least at the top and base of snags where evidence of woodpecker foraging sign was greatest. It is difficult to say whether the absence of bark promotes or is caused by woodpecker foraging.

Arthropod biomass of the entire study tree was significantly correlated with the amount of woodpecker foraging sign ($r = 0.76$, $P < 0.0001$) and specific gravity of snags ($r = -0.49$, $P < 0.001$) but not with pilodyn® measurements of snag hardness ($r = 0.24$, $P < 0.15$). Although not significant, snags that exhibited high use foraging sign had a dry weight arthropod biomass ($\bar{x} = 0.28$ g ± 0.87, $t = 1.23$, $P = 0.23$) more than five times greater than low use snags ($\bar{x} = 0.05$ g ± 0.07). Arthropods collected from study trees included 21 orders: Isoptera (36%), Coleoptera (27%), Hymenoptera (22%), Arachnida (4%), Collembola (3%), Orthoptera (2%), and all others (6%). Most arthropods were collected from the bottom portions of study trees (338 of 532 arthropods).

Observations of foraging woodpeckers.—Although there was considerable foraging sign on the 60 study trees, woodpeckers were only rarely

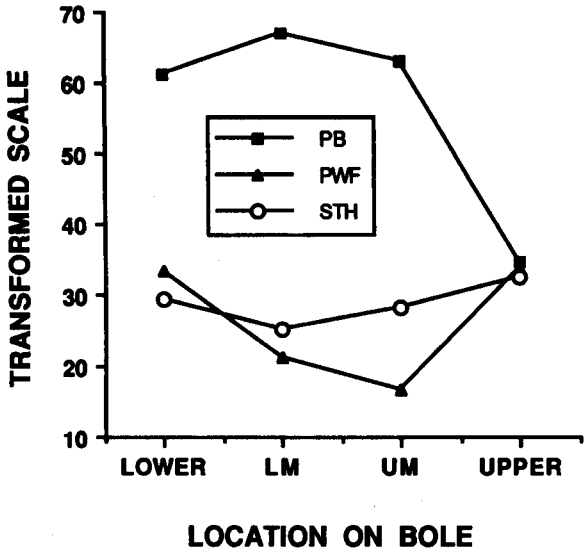

FIG. 1. Percentage of tree surface foraged on by woodpeckers (PWF), percentage of intact bark (PB), and study tree hardness (STH) at the four height zones on snags (lower, lower middle [LM], upper middle [UM], and upper) in the bottomland forest on the Stephen F. Austin Experimental Forest in eastern Texas. Higher values for snag hardness indicate more extensive decay (greater pilodyn® penetration means increasing softness).

observed using them. Live trees (live trees and live trees with dead branches) were selected most often as foraging sites by Downy (N = 189, 45%), Pileated (N = 100, 68%), and Red-bellied (N = 111, 62%) woodpeckers in the bottomland hardwood forest habitat, whereas Red-headed Woodpeckers used live trees the least (N = 250, 48%). Downy Woodpeckers used snags 23% of the time, Pileated's 31%, Red-bellied's 30%, and Red-headed's 48%. When snags and dead portions of live trees are combined, Downy (55%) and Red-headed woodpeckers (80%) foraged mainly on dead wood, whereas Pileated (32%) and Red-bellied (38%) woodpeckers foraged primarily on live wood.

Downy Woodpeckers foraged more on twigs (53%) than Pileated (0%), Red-bellied (5%), and Red-headed (2%) woodpeckers. Pileated (70%) and Red-bellied (75%) woodpeckers mainly selected branches as foraging sites, whereas Red-headed (48%) and Downy (25%) woodpeckers foraged on branches to a lesser extent. Red-headed Woodpeckers (50%) foraged on trunks more often than Downy (23%), Pileated (30%), and Red-bellied (20%) woodpeckers.

Woodpecker species foraged at significantly different heights when us-

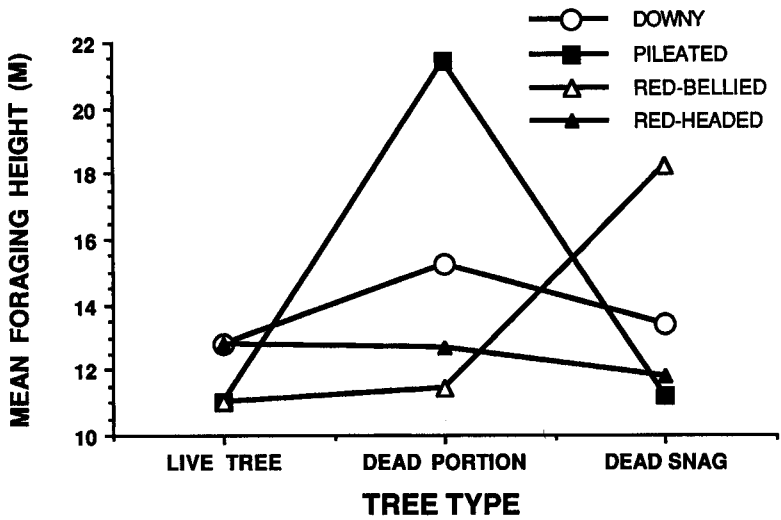

FIG. 2. Mean foraging height in meters of Downy, Pileated, Red-bellied, and Red-headed woodpeckers on live trees, dead portions of live trees, and snags in a bottomland hardwood forest on the Stephen F. Austin Experimental Forest in eastern Texas.

ing different tree conditions (live trees, dead parts of live trees, or snags) (Two-way ANOVA, $P < 0.006$). Downy Woodpeckers used higher sites when foraging on dead parts of live trees and snags than on live trees (Fig. 2). Pileated Woodpeckers foraged at about the same height when foraging on live trees and snags, but used higher sites when on dead parts of live trees. Red-bellied Woodpeckers foraged highest when using snags. Red-headed Woodpeckers varied foraging heights the least when using different tree conditions (Fig. 2).

Downy Woodpeckers foraged upon the largest variety of woody species (Table 6). Pileated Woodpeckers were observed foraging on only four tree species. Bonferroni's test indicated that all woodpecker species preferred to forage on oaks at a higher frequency than their availability and tended to avoid red maples and blue beeches as foraging sites ($P < 0.05$). As also observed by Conner (1979, 1980), Downy Woodpeckers usually stayed at about the same height when moving from tree to tree, typically foraging for a short time period before flying to the next tree. Downy Woodpeckers foraged on the greatest number of tree species as observed by Jackson (1970) and Conner (1980, 1981). Pileated Woodpeckers in our study and others foraged upon the fewest tree species and, in general, appear to be more restrictive in their use of tree species (Bull and Meslow 1977, McClelland 1979, Conner 1981, Kilham 1983).

TABLE 6

PERCENTAGES OF TREE SPECIES FORAGED UPON BY FOUR SPECIES OF WOODPECKERS IN A BOTTOMLAND HARDWOOD FOREST ON THE STEPHEN F. AUSTIN EXPERIMENTAL FOREST

Tree species	Downy	Pileated	Red-bellied	Red-headed
Blue beech	4.5			
Flowering dogwood				4.7
Sweetgum	36.4	33.3	9.1	16.3
Black gum	9.1	13.3	18.2	23.3
Water elm	2.3			
Pine species	4.5	20.0	9.1	4.7
Poison ivy	2.3			
Oak species	34.1	33.4	36.4	37.2
Slippery elm	2.3			
Unidentified snags	4.5		27.3	14.0

Downy Woodpeckers primarily pecked while foraging on twigs of live trees (Fig. 3). Pileated and Red-bellied woodpeckers foraged using the peer-and-poke method more than either pecking or excavating. Red-headed Woodpeckers frequently pecked at substrates while foraging but

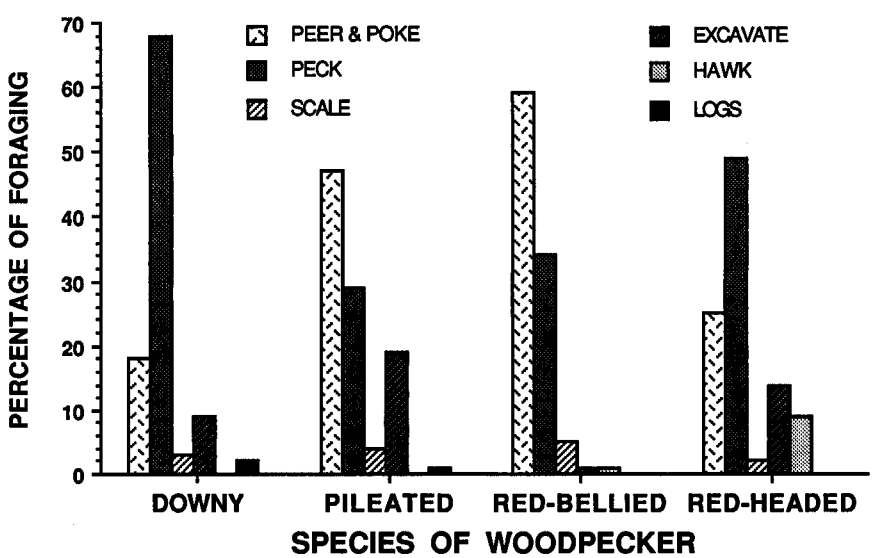

FIG. 3. Frequencies of foraging methods used by Downy (DW), Pileated (PW) Red-bellied (RBW), and Red-headed (RHW) woodpeckers in a bottomland hardwood forest on the Stephen F. Austin Experimental Forest in eastern Texas.

also hawked insects, fed on vegetable matter, and/or foraged on the ground.

DISCUSSION

Both tops and bases of snags were preferred foraging sites for woodpeckers. Ground moisture and flooding at the base of snags and rain soaking the tops may have increased micro-climate humidity and facilitated softening by fungal decay and use by arthropods. Extent of decay appears to be an important indicator of overall snag quality in southern bottomland hardwoods because extent of decay and woodpecker foraging sign were highly correlated with arthropod biomass.

Woodpecker excavations were more frequent on the softer portions of snags, on shorter snags, and on snags in advanced stages of decay in general. This suggests possible relationships among snag age, decay, and height. However, no correlation between snag height and degree of decay was detected (Table 5). Shorter snags are probably older snags (Cline et al. 1980) and would have had a longer time period for decay to occur and woodpeckers to forage on them. However, this would likely be a relatively short period of time in the hot, humid climate of southern bottomland forests because such conditions hasten decay (Cartwright and Findlay 1958, Overholts 1977). Rosenberg et al. (1988) found that woodpeckers had an apparent preference to forage in tall snags in Virginia and that this preference appeared to be the result of a positive diameter–height relationship.

Specific gravity and snag hardness as measured by the pilodyn® (all tree species combined) were highly correlated indicating that pilodyn® measurements are an excellent relative estimate of decay. Previous studies have indicated the similarity of pilodyn® and specific gravity as measures of wood density in forest products studies of undecayed wood samples (Cown 1978, Sprague et al. 1983). We prefer use of the pilodyn® because of its ease of use compared to specific gravity measurements, and it may more closely measure the resistance felt by excavating woodpeckers. However, specific gravity was highly correlated with arthropod biomass whereas pilodyn® measurements were not.

Bark texture (rugosity) within and among tree species may affect arthropod abundance and resulting use of snags by woodpeckers (Jackson 1979). Variability in bark roughness was associated with seasonal differences in foraging behavior of Downy Woodpeckers (Travis 1977). The bark of oaks, black gum, and sweetgum is more deeply fissured than bark of blue beech and red maples. Woodpeckers foraging in the bottomlands on both live and dead trees may have avoided tree species with smooth bark because of a paucity of arthropods.

Oaks were important to foraging woodpeckers both as snags and live trees. Woodpeckers preferentially foraged on oaks and tended to avoid blue beech and red maple. Oaks were among the largest diameter snags in the bottomland whereas blue beech and red maple had the smallest diameters of the most abundant five species of snags (Jones 1987). Although this suggests that tree diameter may have influenced snag selection, results of univariate analyses did not support the importance of large diameter snags as woodpecker foraging sites in southern bottomland hardwood forests. Tree diameter has been shown to be a significant criterion for foraging site selection by woodpeckers in other studies. Mannan et al. (1980), Brawn et al. (1982), and Rosenberg et al. (1988) all found that woodpeckers preferred large diameter snags.

Foraging preferences for particular tree species have been reported in various studies (Willson 1970; Travis 1977; Conner 1980, 1981; Kilham 1983). As in our study, oaks are preferred foraging sites by woodpeckers across a wide range of timber types and geographical regions (Willson 1970, Short 1971, Reller 1972, Williams and Batzli 1979, Conner 1980, Kilham 1983). Oaks in Mississippi had a high (59%) infestation rate of oak borers (Solomon 1969), suggesting the importance of oak borers as a food resource.

Seven species of woodpeckers are indigenous to the bottomland hardwood forest of eastern Texas: Downy, Hairy, Pileated, Red-headed, and Red-bellied woodpeckers, Northern Flicker, and Yellow-bellied Sapsucker. All are permanent residents except the Yellow-bellied Sapsucker which is a winter resident and the Northern Flicker which tends to be migratory. Of these the Downy, Red-bellied, Pileated, and Red-headed woodpeckers, and Yellow-bellied Sapsuckers (winter) are common in the bottomlands whereas Hairy Woodpeckers occur infrequently. Northern Flickers, Yellow-bellied Sapsuckers, and Red-headed Woodpeckers do not normally excavate in trees for food as do other woodpecker species (Reller 1972, Conner 1979, Tate 1973). Because woodpecker species foraging on snags (study trees) were not identified, relationships between snag quality and diameter at breast height that have been observed by others (Mannan et al. 1980, Brawn et al. 1982, Rosenberg et al. 1988) may have been obscured. Also, some of the smaller excavations may have resulted from Tufted Titmouse (*Parus bicolor*) and Carolina Chickadee (*P. carolinensis*) foraging (Conner 1978).

Pileated Woodpeckers in our study foraged more on live trees than generally reported elsewhere (Bull and Meslow 1977, McClelland 1979, Conner 1980). This may reflect a more abundant arthropod community on the surface of live trees in the relatively warm southern forests than the more northerly forests examined in the previous studies. Pileated

Woodpeckers, however, seemed particularly wary of observers, and this may have influenced detection of snag use.

Analyses indicated that snags with extensive foraging sign were found in stands where basal area of live hardwoods, tree diameter, dominant vegetation height, and number of trees greater than 38 cm DBH were high. Collectively, these variables suggest that woodpeckers selected snags that were located in older growth areas, or that preferred snags were found predominantly in older growth areas. Management favoring old-growth bottomland hardwood forests and protection of large diameter oak snags may benefit woodpeckers that forage by excavation. Pileated Woodpeckers excavated more than other woodpecker species in our study area and would benefit the most from provision of large, well decayed oak snags.

ACKNOWLEDGMENTS

We thank J. D. Brawn, D. J. Ingold, J. A. Jackson, R. W. Mannan, M. L. Morrison, and D. K. Rosenberg for helpful comments on an early draft of the manuscript. The mention of trade names in this paper is for the information and convenience of the reader. Such use does not constitute official endorsement or approval by the U.S. Department of Agriculture of any product to the exclusion of other products that may be available.

LITERATURE CITED

BORROR, D. J. AND R. E. WHITE. 1970. A field guide to the insects of America north of Mexico. Houghton Mifflin Co., Boston, Massachusetts.

BRAWN, J. D., W. H. ELDER, AND K. E. EVANS. 1982. Winter foraging by cavity nesting birds in an oak-hickory forest. Wildl. Soc. Bull. 10:271–275.

BULL, E. L. AND E. C. MESLOW. 1977. Habitat requirements of the Pileated Woodpecker in northeastern Oregon. J. Forestry 75:335–337.

BYERS, C. R., R. K. STEINHORST, AND P. R. KRAUSMAN. 1984. Clarification of a technique for analysis of utilization-availability data. J. Wildl. Manage. 48:1050–1053.

CARTWRIGHT, K. ST. G. AND W. P. K. FINDLAY. 1958. Decay of timber and its prevention, 2nd ed. Her Majesty's Stat. Off., London, Great Britain.

CLINE, S. P., A. B. BERG, AND H. M. WIGHT. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44:773–786.

CONNER, R. N. 1978. Snag management for cavity nesting birds. Pp. 120–138 *in* Proc. of the workshop; management of southern forests for nongame birds (R. M. DeGraaf, tech. coord.). U.S. For. Serv. Gen. Tech. Rep. SE-14.

———. 1979. Seasonal changes in woodpecker foraging methods: strategies for winter survival. Pp. 95–105 *in* The role of insectivorous birds in forest ecosystems (J. G. Dickson, R. N. Conner, R. R. Fleet, J. A. Jackson, and J. C. Kroll, eds.). Academic Press, New York, New York.

———. 1980. Foraging habitats of woodpeckers in southwestern Virginia. J. Field Ornithol. 51:119–127.

———. 1981. Seasonal changes in woodpecker foraging patterns. Auk 98:562–570.

COWN, D. J. 1978. Comparison of the pilodyn and torsiometer methods for the rapid assessment of wood density in living trees. New Zeal. J. For. Sci. 8:384–391.

CURTIS, J. T. AND R. P. MCINTOSH. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32:476–496.

EVANS, K. E. AND R. N. CONNER. 1979. Snag management. Pp. 214–224 *in* Management of north central and northeastern forests for nongame birds (R. M. DeGraaf, tech. coord.). U.S. For. Serv. Gen. Tech. Rep. NC-51.

JACKSON, J. A. 1970. A quantitative study of the foraging ecology of Downy Woodpeckers. Ecology 51:318–323.

———. 1979. Tree surfaces as foraging substrates for insectivorous birds. Pp. 69–93 *in* The role of insectivorous birds in forest ecosystems (J. G. Dickson, R. N. Conner, R. R. Fleet, J. A. Jackson, and J. C. Kroll, eds.). Academic Press, New York, New York.

JONES, S. D. 1987. Woodpecker selection of foraging snags in a bottomland forest community of east Texas. M.S. thesis, Stephen F. Austin State Univ., Nacogdoches, Texas.

KILHAM, L. 1983. Life history studies of woodpeckers of eastern North America. Nut. Ornithol. Club, Massachusetts.

KISIEL, D. S. 1972. Foraging behavior of *Dendrocopos villosus* and *D. pubescens* in eastern New York State. Condor 74:393–398.

MANNAN, R. W., E. C. MESLOW, AND H. M. WIGHT. 1980. Use of snags by birds in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44:787–797.

MCCLELLAND, B. R. 1979. The Pileated Woodpecker in forests in the northern Rocky Mountains. Pp. 283–299 *in* The role of insectivorous birds in forest ecosystems (J. G. Dickson, R. N. Conner, R. R. Fleet, J. A. Jackson, and J. C. Kroll, eds.). Academic Press, New York, New York.

MILLER, R. G. 1981. Simultaneous statistical inference. Springer-Verlag, New York, New York.

MORRISON, M. L. AND K. A. WITH. 1987. Interseasonal and intersexual resource partitioning in Hairy and White-headed woodpeckers. Auk 104:225–233.

OVERHOLTS, L. O. 1977. The Polyporaceae of the United States, Alaska, and Canada. Univ. Michigan Press, Ann Arbor, Michigan.

RAPHAEL, M. G. AND M. WHITE. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildl. Monogr. No. 86.

RELLER, A. W. 1972. Aspects of behavioral ecology of Red-headed and Red-bellied woodpeckers. Am. Midl. Nat. 88:270–290.

ROSENBERG, D. K., J. D. FRASER, AND D. F. STAUFFER. 1988. Use and characteristics of snags in young and old forest stands in southwest Virginia. For. Sci. 34:224–228.

SAS INSTITUTE. 1988. SAS/STAT user's guide, release 6.03. SAS Institute Inc., Cary, North Carolina.

SHORT, L. L. 1971. Systematics and behavior of some North American woodpeckers, genus *Picoides* (Aves). Bull. Amer. Mus. Nat. Hist. 145:1–118.

SMITH, D. M. 1954. Maximum moisture content method for determining specific gravity of small wood samples. U.S. For. Serv. Misc. Pub. No. 2014. Madison, Wisconsin.

SOLOMON, J. D. 1969. Woodpecker predation on insect borers in living hardwoods. Ann. Entomol. Soc. Am. 62:1214–1215.

SPRAGUE, J. R., J. T. TALBERT, J. B. JETT, AND R. L. BRYANT. 1983. Utility of the pilodyn in selection for mature wood specific gravity in loblolly pine. For. Sci. 29:696–701.

TATE, J., JR. 1973. Methods and annual sequence of foraging by the sapsucker. Auk 90: 840–856.

THOMAS, J. W., R. G. ANDERSON, C. MASER, AND E. L. BULL. 1979. Snags. Pp. 60–77 *in* Wildlife habitats in managed forests, the Blue Mountains of Oregon and Washington (J. W. Thomas, tech. ed.). U.S. For. Serv. Agric. Handbk. No. 553.

TRAVIS, J. 1977. Seasonal foraging in a Downy Woodpecker population. Condor 79:371–375.

U.S. FISH AND WILDLIFE SERVICE. 1984. Texas bottomland hardwood preservation program, category 3. U.S. Fish and Wildl. Serv., Albuquerque, New Mexico.

U.S. SOIL CONSERVATION SERVICE. 1980. General soil map, Nacogdoches County, Texas. U.S. Soil Cons. Serv. Fort Worth, Texas.

WILLIAMS, J. B. AND G. O. BATZLI. 1979. Competition among bark-foraging birds in central Illinois: experimental evidence. Condor 81:122–132.

WILLSON, M. F. 1970. Foraging behavior of some winter birds of deciduous woods. Condor 72:169–174.