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HABITAT AND TERRITORIAL REQUIREMENTS OF THE YELLOW-BELLIED SAPSUCKER ON NESTING AREAS IN NORTHERN MICHIGAN

bу

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B.A., Albion College

A Thesis

Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Arts in Biology

School of Graduate Studies

Northern Michigan University

Marquette

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The members of the Committee appointed to examine the thesis of Douglas B. Wilde find it satisfactory and recommend it be accepted.

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ABSTRACT

Nine nesting trees of Yellow-bellied Sapsuckers (Sphyrapicus varius varius) were examined in Marquette County, Michigan. One hundred feed trees from six areas were also examined. Nesting always occurred in dead wood, usually isolated from the surrounding canopy. Open water was present in each area. Nine species of feed trees were found. Feed trees tended to be larger than non-feed trees. The density of trees did not appear to influence the sapsucker density. The amount of solar radiation and water available to a tree apparently helps determine its "attractiveness" to the sapsucker. Those factors which tend to increase the vigor and value of a tree from the standpoint of lumber also make the tree more prone to sapsucker attack. Hypothetical search images and selection mechanisms for nest and feed tree are detailed.

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INTRODUCTION

The sapsucker (Sphyrapicus varius) is a common bird over much of the North American continent. It is considered to be a polytypic species with four well characterized subspecies (Howell, 1952), which have diverged only recently (Short, 1970). These four subspecies are: Sphyrapicus varius varius (Yellow-bellied Sapsucker), S. v. nuchalis (Red-naped Sapsucker), S. v. ruber (Red-breasted Sapsucker), and S. v. daggetti (Red-breasted Sapsucker). Of these four, the yellow-bellied sapsucker undergoes the longest migrations and occupies the largest breeding range: from southern Ohio to Arkansas to northern Canada and from Newfoundland to British Columbia (Howell, 1953).

The yellow-bellied sapsucker (<u>S. v. varius</u>) is the only subspecies present in the Great Lake states, where it is a regular summer resident. In the Upper Peninsula of Michigan the males arrive in mid-April, establish a nesting territory, attract a mate, and then both adults rear their young. They stay on their breeding grounds until late September or early October before migrating south.

Trees provide the sapsucker with two essential requirements for life: food and shelter. The sapsucker will nest only in areas that contain trees suitable for both purposes. Whereas insects are an important component in woodpecker diets, sap and bast material (the cork cambium and phloem) also make up a significant part of the sapsucker's diet (Bolles, 1892; Beal, 1922; McAtee, 1911). Sap is obtained by drilling holes through the cambium layer of woody plants

and lapping up the sap that is discharged from these wounds. Bast, which has considerable food value at some seasons (Tate, 1973), is also obtained from these holes. Sapsucker damage is easily recognized for it is the only woodpecker in the Great Lakes area whose drilling is ordered in rows and columns. Holes are generally rectangular, with sap holes clean and square, and bast holes having ragged edges.

The sapsucker uses a wide variety of plants as food sources. McAtee (1911) has named 288 species of woody plants that were damaged by feeding sapsuckers. The extent and type of damage sapsuckers inflict on trees in obtaining sap and bast has been studied (e.g., Bolles, 1891; Danforth, 1938; McAtee, 1911; Lockland, 1963), the most recent and thorough by Tate (1973). This type of damage not only leads directly to tree death because of girdling (Ziller, 1961; Kilham, 1964; Shigo, 1963) but also sets up conditions allowing infections which reduce tree vigor (Ohman, 1964). Tree mortality can be as high as 67% of those trees drilled (Rushmore, 1969). It has been found that the species of tree utilized on the nesting area change as the season progresses (Foster, 1966; Kilham, 1964; Rushmore, 1969; Tate, 1973). The probable reason for this shift in food tree preference is due to leafing out of desired food species and the commencement of photosynthesis. Conifers, which have sap flow in the early spring, serve as the main food trees until sap flow starts in the deciduous species.

The sapsucker is a territorial bird with each family unit developing its own feed trees (Howell, 1952; Kilham, 1962; Rushmore, 1973). Both adults tend the young but only the male roosts at night in the nest tree (Johnson, 1947). There has been much discussion

on the distribution of the feed trees within territories, with these trees tending to be scattered in spring and fall while in summer a single stand of trees, called an "orchard," provides all the sap for one family (e.g., Bolles, 1891; Foster, 1966; Tate, 1973).

Little work, however, has been done on the characteristics of feed trees (Cahn, 1920; Kilham, 1953; 1964). The relationships between feed trees and other trees in the territory has not been examined.

Oliver (1968) compared feed and non-feed trees with regard to bark thickness, DBH, relative vigor and dominance and found no significant differences between them.

Sapsuckers use a variety of tree species for nesting, including birches (Betula spp.), poplars (Populus spp.), elms (Ulmus spp.), butternut (Juglans cinerea), and occasionally conifers such as the red pine (Pinus resinosa) (e.g., Bendire, 1888; Hicks, 1933; Jackson, 1923; Mousley, 1916; Tatschl, 1967; Wible, 1966). The nest is built in a cavity the bird excavates, approximately 30 cm deep with an entrance hole 3.8 cm in diameter. Often nests are built in dead trees or in dead stubs and branches (e.g., Bent, 1939; Howell, 1952; Kilham, 1962; 1971; Philipp, 1917). Live trees, when occupied, may have heart rot which permits easier excavation. This rot is often caused by the fungus Fomes igniarius (Kilham, 1971; Shigo, 1968).

One distinguishing characteristic often present on sapsucker nest trees is multiple nest cavities (e.g., Erskin, 1972; Kilham, 1962; 1971; Mousley, 1916). This is caused by sapsuckers renesting in the same tree, usually in a new cavity (Kilham, 1971). It has also been noted that sapsuckers start three to four holes each year before settling upon the final nesting cavity (Howell, 1952; Kilham, 1972).

The height at which the nests occur varies widely, with extremes reported of 5 to 60 feet (1.5-18.3 m) and an average of between 20 and 40 feet (6.1-12.2 m) (e.g., Bendire, 1888; Foster, 1966; Johnson, 1947; Philipp, 1917; Tatschl, 1967), although Erskine (1972) measured a mean height of from 10 to 20 feet (3-6.1 m) in aspens (Populus spp.).

Kilham (1971) maintains that the holes are located in those portions of trees that have a straight bole and diameter of 8 to 10 inches (20-25 cm) for aspen, agreeing closely with the diameter of 9 inches (22.9 cm) found by Erskine (1972). The nest hole entrance measures 1.5 to 1.625 inches (3.8-4.1 cm) in diameter (Erskine, 1972).

There appears to be no differences in the individual statistics (DBH, bark thickness, relative vigor and dominance) of feed and nonfeed trees. Nest trees may be more easily distinguished since dead segments of trees or those with heart rot are often used. This may indicate that external characteristics of a tree and the surrounding area influence sapsucker selection of trees. The North Central Forest Experiment Station of the U. S. Forest Service in Marquette, Michigan is conducting yellow birch (Betula alleghaniensis Britton) crown release thinning studies where all competing trees whose crowns are within specified distances (5, 10, or 15 feet; 1.5, 3.0 or 4.6 meters) of a selected tree's crown perimeter are removed. In these studies, sapsucker feeding on yellow birch appeared to be related to the degree of release with the most extensive feeding occurring on the wider (10 and 15 foot; 3.0 and 4.6 meter) crown release treatments (Erdmann and Oberg, 1974).

The removal of the surrounding crown cover apparently made these trees more "attractive" to the sapsucker. This increased

"attractiveness" may be due to changes in the endogenous characteristics of the tree, such as increased sap flow or a better quality sap following crown release treatment. Increased use of crown released trees by the sapsucker may also be due to the sapsucker's behavior, e.g., such trees require the sapsucker to expend less energy in food gathering. In this case, the removal of the surrounding crown makes it easier for the sapsucker to approach the tree. Therefore, a complete description of a sapsucker feed or nest tree may require quantitative examination of the immediate surrounding area.

Other features, besides suitable feed and nest trees, may be necessary to fulfill the nesting requirements of a pair of sapsuckers. Two such characteristics mentioned in the literature are proximity of water or swampy areas (e.g., Bendire, 1888; Foster, 1966; Kilham, 1971; Philipp, 1917; Ardrich, 1934) and openings in the canopy (Davison, 1888; Howell, 1952). If the characteristics of an area which are necessary for sapsucker nesting can be described, habitat management practices may be initiated to decrease sapsucker damage.

The purpose of my study was to describe and analyze the ecological characteristics of nests, feed trees, and nesting area of yellow-bellied sapsuckers in the Upper Peninsula of Michigan. Specific objectives were:

- 1) To determine physical features of nest trees.
- 2) To identify essential features of feed trees and determine whether sapsuckers have preferences for certain features.
- 3) To observe behavior to see if this could provide clues regarding area and tree selection by the sapsucker.

4) To determine what other physical characteristics were necessary in the nesting area, such as a proximity to water and openings in the canopy around the nest and/or feed tree.

STUDY AREA

Nine nesting trees from three areas within Marquette County in the Upper Peninsula of Michigan were examined (Fig. 1). This included six nesting trees at the Upper Peninsula Experimental Forest, two at the McCormick Experimental Forest and one at the Huron Mountain Club. Appendix 1 contains a detailed listing of the trees found at each nest tree studied.

The Upper Peninsula Experimental Forest is maintained by the Northern Hardwoods Laboratory, North Central Forest Experiment Station, USDA Forest Service. A study on the Forest involving improvement in yellow birch growth rates prompted this study (Erdmann and Oberg, 1974). The six nesting trees studied here were scattered throughout the Forest. Three trees (OT, MS, and MSS) were located near a spur road leading to the Marking School area. Another tree, DUKE 1, was at the end of another spur road and adjacent to yellow birch studied by Erdmann and Oberg (1974). A fifth tree, M-94 in the southwest corner of the forest, was also located near an abandoned logging road. The remaining nesting tree, CURVE, was located off the main forest road, also in the southwest corner.

The McCormick Experimental Forest encloses 17,124 acres (6932 ha) that have been disturbed little since 1936. An inventory of animals by Robinson and Werner (1975) was recently conducted. The vegetation of the northeast corner of the forest has also been described (Metzger, 1973). The two nesting trees examined in this forest, YD and LB, were

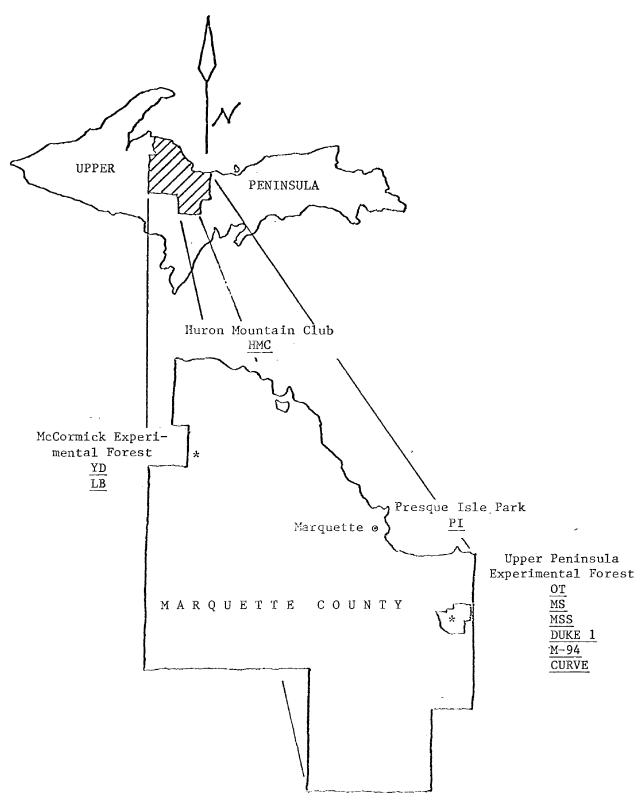


Figure 1. Locations of study areas within Marquette County, Michigan. Underlined names indicate specific study areas.

located in the northeast and southwest corners, respectively. YD was located near the Yellow Dog River whereas LB was found on the east shore of Lower Baraga Lake.

The Huron Mountain Club is 17,000 acres (6911 ha) of forest and Lake Superior shoreline maintained in a natural state for use by club members. The nesting tree studied in this area (HMC) was located in the middle of the club's eastern boundary, along the banks of the Salmon-Trout River. A detailed account of the animals and plants of this area can be found in studies by Laundre' (1975) and Westover (1971).

Feed trees were examined in all three areas that contained the nesting trees. Additionally, a fourth area, Presque Isle Park, was also used. Although the park is located within the city limits of Marquette, Michigan and contains a stand of mixed hardwoods, the feed trees measured came from a picnic-park area. Saplings and undergrowth, other than a maintained lawn, were absent.

METHODS AND MATERIALS

Location of Trees

Locating nest trees was accomplished in two ways. Sections of woods presumably occupied by sapsuckers were first located primarily by walking and driving down logging roads and trails, looking for sapsucker damage and listening for sapsucker drumming. In early spring sapsuckers call, drum, or tatoo on trees, primarily to delineate territory and attract a mate (Bolles, 1891; Howell, 1952; Kilham, 1962). If a sapsucker was heard or fresh damage located, an imitation of the tatoo was rendered by rapping a stick against a convenient dead limb, a variation on a technique described by Rushmore (1973). The sapsucker usually answered and flew over to investigate, thus revealing the general location of its territory.

In late spring during the incubation period, sapsuckers are usually quiet (Hicks, 1933). Except for one instance, I was able to find the exact location of nests only after the young had hatched and started to vocalize. The young are very noisy, putting up a constant ruckus which can easily be heard, often increasing in intensity when an adult returns (Bolles, 1892).

Feed trees were located either by following adults which were feeding young on the nest, or by searching the area around a nest tree. Feed trees which had been located while searching for nest trees were also measured.

Nest Tree Data

Data were collected to describe the nest tree and trees surrounding it. Each nest tree was identified to species, if living, and its general condition (living, dead, dead stub) was noted. That section of tree occupied by the nest and the condition of that section was recorded (living, dead—with or without bark, dead stub, trunk, side branch) as well as the presence of other sapsucker damage on the tree. The distance and direction of water (pond, lake, swamp, stream) was recorded.

The diameter at breast height (DBH) of the nest tree was measured with a diameter tape. Diameter of the bole at nest height (DNH) and nest entrance diameter (NED) were measured by a Barr and Stroud Dendrometer. The height of the nest entrance was calculated using an Abney level and meter tape, the position of the nest in relation to the general forest canopy (below, in or above) and compass heading of the nest entrance was noted.

Using the nest tree as the center, a 10752.7 ft² (1000 m²) circular plot was established. This provided a sample of trees within a radius of 58.5 ft. (17.8 m) which could be compared to the nest tree. All trees greater than 4 inches (10.2 cm) DBH were sampled. This division is arbitrary but made for two reasons: 1) trees of this size are not frequently used by the sapsucker (Tate, 1973) and 2) to reduce the number of trees to be measured, by eliminating saplings. The species, DBH, distance and direction from nest tree, condition (living, dead), and sapsucker damage (if present) of each tree in the sample plot was recorded.

Preliminary examination of the nesting areas suggested that openings in the canopy around the nest hole were important. The distance to a vertical projection of the canopy at nest height was measured at 45° intervals, starting with the nest hole as 0°. Additional openings of the canopy in the immediate area were also noted.

Feed Tree Data

Similar data were collected on feed trees as from nest trees. Species and DBH of each feed tree were recorded. Sapsuckers drill holes differing in shape and arrangement depending upon time of year, extent of use, and material being extracted. Injury to trees was classified as columns, bands, scattered, or a combination of these (Tate, 1973), and divided into new (of the year of measurement) or old (of a previous year) injury. Trees were also classified regarding the extent of sapsucker injury incurred. Instead of total counts of holes (some trees may have over 6000 holes; Kilham, 1964), the trees were aribtrarily divided into three categories: LIGHT INJURY (1 band, column, or approximately 10 scattered holes), INTER-MEDIATE INJURY (2-5 bands, 2-5 columns, or 10-20 scattered holes), and HEAVY INJURY (>5 bands, >5 columns, or >20 scattered holes). Trees with LIGHT INJURY are used only infrequently and often just once, perhaps by transient birds. A tree with INTERMEDIATE INJURY may be revisited and used intermittently but the feeding does not seriously injure the tree. HEAVY INJURY indicated a major feed tree and frequent use. This type of heavy use usually affects the tree's vigor, often reducing growth (Erdmann and Oberg, 1974) or

causing the top to die above girdles and even death of the entire tree. Other injury to the tree by other animals, fungi, or mechanical injury was also recorded. As with nest holes, the crown position of the feed tree and the location of sapsucker injury (below, in, or above the canopy) was noted. Using the feed tree as the center, a 2150.5 ft² (200 m²) circular plot was laid out and all trees larger than 4 inches (10.2 cm) DBH were recorded as to species, DBH, condition and whether there was sapsucker injury present. Finally, if water was within sight of the feed tree, its distance and direction were noted.

Behavioral notes were made on the birds from the time of nest excavation to fledging of the young. These observations could provide possible explanations for the selection of certain trees and areas for nesting and feeding. Observations included insect captures by sapsuckers, flights around the nest tree, and frequency of feeding the nestlings.

RESULTS

Nest Tree

Nine nest trees were located and examined. Individual measurements are presented in Table 1. The height of the nest hole and DBH were not recorded for one nest (DUKE 1) because the tree was blown down between the time it was located and when measurements would have been taken. The DBH of the remaining trees varied greatly. The mean DBH was 15.6 inches (39.8 cm), with a standard deviation of 5.3 inches (13.6 cm).

The diameter at nest height (DNH) was smaller and less variable than the DBH. Mean DNH was 7.7 inches (19.5 cm). The minimum diameter was 6.3 inches (16.0 cm).

The nest entrance diameter (NED) is even less variable, the mean diameter being 1.4 inches (3.7 cm). The standard deviation was only 0.2 inches (0.6 cm).

The height at which nests occurred was quite variable. The minimum height was 10.8 feet (3.29 m) whereas a maximum of 55.6 feet (16.95 m) was measured at nest tree MSS. The mean height of all nests was 35.0 feet (10.67 m).

Nest entrance directions tended to be clumped, but not significantly so ($X^2=7.22$, DF=3, 0.10>P>0.05). Four entrances were in the southwest quarter ($180^\circ=270^\circ$) and four in the northwest ($270^\circ-360^\circ$) and none were found between 90° and 180° (Fig. 2).

The condition of the nest trees is summarized in Table 2. All nests were located in dead trees or dead branches of living trees.

Seven nest trees had additional nest holes, but it is not known how

TABLE 1

MEASUREMENT OF NEST TREES

NEST	SPECIES	DIAMETER AT BASE HEIGHT (inches)	DIAMETER AT NEST HEIGHT (inches)	NEST ENTRANCE DIAMETER (inches)	HEIGHT OF HOLE (feet)	DIRECTION OF HOLE (degrees)
M-94	White Birch	9.7	7.3	1.5	7.1	89
LB	:	15.7	12.6	1.4	23.2	63
CURVE	Sugar Maple	12.4	5.8	1.3	42.1	257
MS	=	10.1	9.9	1.4	10.8	213
MSS	:	20.4	7.9	1.2	55.6	188
OT	:	19.9	6.3	1.2	57.2	2
ΥD	:	24.3	7.3	1.7	36.4	87
DUKE 1	:		6.3	1.5	an en en en	246
HMC	Basswood	12.8	9.2	1.7	33.1	305
	MEAN	15.6	7.7	1.45	35.0	
	STANDARD DEV.	5,35	2.10	0.19	16.35	
	SAMPLE SIZE	8	6	6	∞	

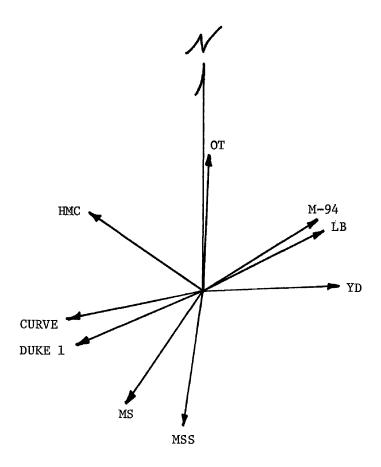


Figure 2. Direction of nest entrance openings.

TABLE 2

CONDITION OF NEST TREE AND NEST

NEST TREE	SPECIES	CONDITION OF TREE	CONDITION OF NEST	BARK AT NEST	LOCATION OF NEST	OTHER
76-W	White Birch	DEAD	DEAD	YES	STUB	3 NEST HOLES
LB	:	DEAD	DEAD	YES	TRUNK	NONE
CURVE	Sugar Maple	LIVE	DEAD	NO	BRANCH	2 NEST HOLES
MS	=	DEAD	DEAD	YES	STUB	NONE
MSS	=	LIVE	DEAD	NO	BRANCH	2 NEST HOLES
OT	=	LIVE	DEAD	NO	BRANCH	OTHER HOLES
χD	:	DEAD	DEAD	NO	TRUNK	OTHER HOLES
DUKE 1	=	DEAD	DEAD	NO	TRUNK	OTHER HOLES
HMC	Basswood	DEAD	DEAD	YES	STUB	FEED BANDS

many of these holes represented nest cavities that had been used by sapsuckers.

Openings around the nest tree were analyzed in two ways. The mean canopy distance at the nest hole and 45° either side of the hole was compared to the mean canopy distance at the remaining sample angles. The results are contained in Table 3. Only one tree, OT, exhibited a significant difference between the two means. The distance of canopy from the nest hole was significantly greater than around the rest of the nest tree. At half of the remaining trees the distance from the surrounding canopy to the nest was greater, though not significantly so.

The trees with old nest holes were also examined to determine if there had previously been openings in the canopy. Sapsuckers exhibit fidelity to a nest site, often reinhabiting the same tree (Kilham, 1971). An opening in the canopy around a tree in the past may have induced sapsuckers to nest in that tree. Site fidelity would cause the birds to continue to nest in this tree, even though the canopy had since closed up. If trees had been removed from around the nest tree, those growing closest to the nest tree should be smaller. Regressions were run comparing the basal area of the surrounding trees to their distance from the nest tree. All trees within the 1000 m² plot were handled thus and the results presented in Table 4.

All equations produced low linear and parabolic r values, ranging from 0.00 for OT to 0.39 at YD and DUKE 1. Whereas this r is low for YD and DUKE 1, it is significantly different from zero, for the parabolic equation. This would indicate a lack of trees near

TABLE 3

COMPARISON OF CANOPY OPENING AT NEST AND 45° EITHER SIDE OF THE NEST OPENING, AND THE REST OF THE CANOPY AROUND THE NEST TREE

NEST O	OPEN TO	MEAN DISTANCE OF CANOPY WITHIN 45°	MEAN DISTANCE OF REST OF CANOPY	DF	t t
CURVE	YES	7.62 ш	6.95 ш	9	0.16
LB	NO	3.05	1.05	9	1.60
χD	YES	5.69	4.30	9	0.77
HMC	YES	13.67	16.11	9	08.0
DUKE 1	YES	8.13	69.6	9	0.91
M~94	NO	0.39	0.97	9	1.67
OT	YES	11.89	0.91	9	4.36**
MSS	NO	1.15	2.13	9	1.01
MS	NO			1	

**p<0.01

TABLE 4

REGRESSION OF TREE BASAL AREA AGAINST DISTANCE AWAY FROM THE NEST TREE

NEST TREE	NUMBER OF TREES	DF	LINEAR r	PARABOLIC r	SLOPE = 0
MSS	41	39	0.2	0.22	YES
OT	29	27	0.0	0.00	YES
CURVE	42	40	0.2	0.26	YES
DUKE 1	43	41	0.1	0.39	NO
M-94	59	57	0.2	0.22	YES
YD	31	29	0.2	0.39	NO
HMC	24	22	0.0	00.00	YES

the nest tree or that trees closest to the nest tree are smaller, i.e., younger.

Trees were also examined with regard to openings in the canopy over the nest tree (Table 3). For five of the nine trees (55%) the canopy did not extend over the nest tree. MS, one of the remaining four trees, had a space of at least 15 feet (4.57 m) between the tree's top and the lower limit of the canopy. Other openings in the canopy or forest were found and are summarized in Table 5.

Water was found within each nesting area, i.e., that area occupied by a nesting pair of sapsuckers. The findings are summarized in Table Some additional comments are necessary. The swamp at MSS was due to the impounding of a small stream. This covered an extensive area to the east of the nest. The swamp at OT was due to flooding by a small intermittent stream. The flooding that caused this swamp was more localized than at MSS, and water was present all year whereas the OT stream dried up occasionally. The ponds at DUKE 1 were maintained by beavers, water coming from a large swamp located south of the nest tree. Although the swamp at CURVE was located 440-550 yards (400-500 m) from the nest, only 110 yards (100 m) of this distance was wooded, the remainder being open meadow. In addition to the two swampy areas at M-94, a large swamp was located to the northeast. This swamp was too impassable and large to be examined for sapsucker use. Lastly, the marsh at LB bordered Lower Baraga Lake.

Feed Trees

One hundred feed trees, largely from four areas, were examined.

At LB, 26 feed trees were measured, 22 at MSS, 27 at MS, and 18 at PI.

TABLE 5

OPENINGS IN THE CANOPY AROUND THE NEST TREE OR IN THEIR VICINITY

AREA	ACCESS ROAD	LOGGING ROAD, CANOPY CLOSED OVERHEAD	SWAMP LAKE	STREAM RIVER	MEADOW	DEAD
MS	YES					
MSS		YES	YES			
OT	YES		YES			
CURVE	YES	YES			YES	
DUKE 1	YES					
M-94		YES				
LB			YES	YES		YES
X.D				YES		
НМС	YES			YES		YES

TABLE 6

PRESENCE OF WATER AROUND NEST TREES

SWAMP		$\rm YES^1$	${\rm YES}^1$	YES		YES			
MARSH							YES^2		
STREAM-RIVER								YES (TWO)	YES
POND	YES (TWO)				YES				
LAKE							YES		
NEST TREE	MS	MSS	OT	CURVE	DUKE 1	M-94	LB	αx	НМС

 $^{\mathrm{l}}$ Swamp present around stream

 $^{^2{\}rm Marsh}$ present on edge of lake

In addition, two trees from M-94 and four from HMC were included in the sample. The species are listed in Table 7.

The mean basal area of all feed trees at each study area was calculated. These values were used to determine if the feed trees among the areas were the same size. The results are presented in Table 8. The size of feed trees at MS and MSS were very similar. By the same token, feed trees at LB and PI were not significantly different. However, when feed trees at MS and MSS were compared to those at LB and PI, feed trees from the former were significantly larger than the latter. Since feed trees can differ significantly in size depending upon the area in which they are located, trees should not be indiscriminately lumped by species with no regard for the tree's place of origin. Differences in size may be due to species composition of the sample (feed trees) or to the age of the trees.

The four areas were then compared at the species level to see if feed trees of the same species were the same size. The results are listed in Table 9. Basswood was significantly larger at MS compared to MSS. PI sugar maple feed trees were significantly smaller than those at MS and MSS. All other comparisons were not significant. Although the majority of the comparisons indicate that feed tree size (basal area) is similar within a species, the results of sugar maples at PI and MS-MSS show that sapsuckers are utilizing those trees that are available. Since all PI feed trees were significantly smaller than those at MS-MSS (see Table 8), one would also expect sugar maples to be smaller.

The basal areas of each feed tree species were then compared

TABLE 7

FEED TREES AND THEIR PERCENTAGES
AT FOUR STUDY AREAS

AMER. BALSAM TOTAL ELM FIR NUMBER	(4%) 27	22	(3%) 26	
RED OAK	ŀ	}	ł	
YELLOW BIRCH	[1	(8%)	
WHITE BIRCH	1		(20%)	
BASS- WOOD	(7%)	(23%)	1	
RED MAPLE		1	(31%)	
SUGAR MAPLE	(%68)	(77%)	(8%)	
AREA	MS	MSS	LB	

TABLE 8

COMPARISON OF MEAN FEED TREE
BASAL AREA AMONG AREAS

		MEAN :	BASAL AREA	NUMBER		
STUD	Y AREAS	IN ²	(CM ²)	OF TREES	DF	t
MS		239	(1482.3)	27	F-1	5 (04)
LB	vs.	85	(551.1)	26	51	5.68**
MS PI	vs.	239 99	(1482.3) (647.5)	27 19	44	4.39**
11		,,,	(047.5)	17		
MSS LB	vs.	279 85	(1804.8) (551.1)	22 26	46	3.86**
				-		
MSS PI	vs.	279 99	(1804.8) (647.5)	22 19	39	3.05*
MSS MS	vs.	279 239	(1804.8) (1482.3)	22 27	47	0.93
110		234				
LB PI	vs.	85 99	(551.1) (647.5)	26 19	43	0.81

^{*}p<0.01

^{**}p<0.001

TABLE 9

COMPARISON OF BASAL AREAS OF FEED TREE SPECIES AMONG THE STUDY AREAS

FEED TREE			MEAN BASAL AREA		NUMBER		
SPECIES	AREA	3A	IN^2		OF TREES	DF	4
White Birch	PI LB	·s⁄a	79 86	(509.3) (554.4)	5 13	16	0.29
Basswood	MSS MS	VS.	104 144	(676.4) (931.4)	rJ 93.	5	2.65*
Sugar Maple	MSS MS	vs.	331 235	(2136.8) (1518.6)	17 24	39	1.57
	MSS LB	VS.	331 130	(213 6. 8) (837.8)	17 2	17	1.05
	MS LB	vs.	235 130	(1518.6) (837.8)	24 2	24	1.18
	LB PI	vs.	130 47	(837.8) (312.5)	2 5	5	1.37
	MSS PI	vs.	331 47	(2136.8) (312.5)	17 5	20	2.36*
	MS PI	vs.	235 47	(1518.6) (312.5)	24 5	27	3,39**
Hemlock	M-94 HMC	vs.	76 141	(489.8) (90 6. 6)	3.2	æ	0.97

*p<0.05, **p<0.01

at each study area to determine if feed trees within an area are
the same size. The results are presented in Table 10. Of the eleven
comparisons made among the four areas, only four were significant.

At PI, red oaks were significantly larger than sugar maples. The
only other significant differences occurred at LB. Red maples were
significantly smaller than white and yellow birches. Additionally,
yellow birch was significantly larger than white birch. Once again,
most feed trees were of similar size, regardless of species. The
exceptions, red oak at PI and red maple at LB, are due to differences
in size of the trees available to the sapsucker. Red oaks, in general,
are larger than the sugar maples at PI and red maples are smaller
than the yellow or white birches at LB.

The basal area of feed trees and non-feed trees in the same study area were then compared to determine whether sapsuckers were chosing trees because of their size. Table 11 contains the results. Sugar maples that were utilized by sapsuckers at MS and MSS were significantly larger than the sugar maples not used. This is also true for basswood at MSS. A comparison for basswood at MS was not possible because all basswood in the 200 m² plots were used by the sapsuckers. At this area the basswood ranged from 10.0 to 12.6 inches DBH (506.4 to 804.0 cm² basal area).

The only other significant difference observed between feed and non-feed trees occurred at LB. The balsam fir utilized was significantly larger than the non-feed balsam fir. The eight other comparisons were not significant. In 10 of the 12 comparisons, the feed trees were larger than the non-feed trees. Sapsuckers therefore tend to feed upon the larger trees available to them.

COMPARISON OF FEED TREE BASAL AREAS BY SPECIES AT EACH STUDY AREA

TABLE X

STUDY AREA	FEED TREE SPECIES	IN	MEAN BASAL AREA (CM ²)	NUMBER OF TREES	DF	rt
Ιď	WB SM Vs.	79 47	(509.3) (312.5)	៤ ៤	œ	0.98
	WB RD VS.	79 141	(509.3) (910.4)	9 5	12	1.94
	RD vs. SM	141 47	(910.4) (312.5)	5 7 9	12	3.26**
LB	RM Vs.	46 130	(300.7) (837.8)	2 8	8	1.96
	RM vs.	46 86	(300.7) (554.3)	8 13	19	2.55*
	RM vs.	46 202	(300.7) (1297.3)	2 8	8	9.31***
	WB Vs.	86 202	(554.3) (1297.3)	13 2	13	3.94**
	WB vs.	86 130	(554.3) (837.3)	13 2	13	1.06
	YB SM vs.	202 130	(1297.3) (837.3)	2 2	2	0.71
SW	SM vs.	121 144	(777.8) (931.4)	24 2	24	1.05
MSS	SM vs.	331 104	(2136.8) (676.4)	17 5	20	1.89
*p<0.02,	**p<0.01,	***p<0.001				

TABLE 11

COMPARISON OF FEED TREE TO NON-FEED TREE BASAL AREAS BY SPECIES IN EACH STUDY AREA

STUDY	FEED TREE	MEAN BASAL AREA	, AREA	NUMBER		
AREA		IN ²	(CM ²)	OF TREES	DF	t
MSS	Sugar Maple	331	(2136.8)	17	,	
		107	(686.9)	69	84	4*96.4
	Basswood	104	(676.4)	5		
		36	(232.6)	7	7	5.98**
MS	Sugar Maple	235	(1518.6)	24		
		95	(613.5)		206	6.53**
PI	White Birch	79	(509.3)	5		
		73	(472.2)	7	7	0.14
	Red Oak	141	(910.4)	6		
		27	(146.2)	2	6	0.93
	Sugar Maple	7.7	(312.5)	5		
		30	(197.2)	11	14	1.55
TB	Red Maple	46	(300.7)	∞		
		36	(243.1)	33	39	1.01
	White Birch	98	(554.3)	13		
		92	(593.3)	31	42	0.28
	Yellow Birch	202	(1297.3)	2		
		143	(923.0)		\leftarrow	3,33
	Sugar Maple	130	(837.8)	2		
		119	(771.3)	80	&	0.10
	Balsam Fir	69	(447.5)	г⊣		
		24	(157.4)	5	4	2.60*
HMC	Hemlock	140	(906.6)	e,		
		397	(2565.3)	5	9	1.32

*p<0.01, **p<0.001

To see if more trees were being utilized by sapsuckers as tree size and tree density increased, the total basal area of trees within each plot was regressed on the number of trees with sapsucker injury. Additionally, the number of trees within each plot was regressed on the number of trees with sapsucker injury. The results are contained in Table 12. Only those feed tree species with three or more trees in an area were used in these calculations, thus only sixteen regressions were calculated. Only three resulted in lines whose slope was significantly different from zero, indicating that a relationship existed. These involved two species of feed trees, each in a different study area. This indicates that generally, increasing the number of trees available in a given area does not mean more trees will be utilized by sapsuckers. However, in certain circumstances, an increase in tree density may increase the number of trees utilized. The opposite, decreased number of trees per area used as tree density increases, did not occur.

A regression was run on the number of tree species in a study area against the number of feed tree species. A parabolic line fit with a r value of 0.97. This is significantly different from zero at the 5% level. It therefore appears that more species are utilized when more are available.

Sapsucker damage was found on nine species of trees (Table 13). In all but one species, red maple, at least 50% of the feed trees sustained heavy injury.

Table 14 lists those feed trees examined that exhibited new sapsucker injuries. None of the red oak, red maple, or American elm that were examined had evidence of new injury. A $\rm X^2$ test ($\rm H_{\odot}$:

TABLE 12

REGRESSION ANALYSIS OF TOTAL BASAL AREA OR NUMBER OF TREES
PRESENT IN PLOT TO THE NUMBER OF TREES
DAMAGED BY SAPSUCKERS

AREA	SPECIES OF FEED TREE	DF	LINEAR r VALUE BASAL AREA N	UMBER	SLOPE = 0
	Sugar Maple	22	0.26	00.0	YES
	Sugar Maple	15	0.14	0.10	YES
	Basswood	ю	0.82	.89*	YES
	Red Maple	9	0.00	0.41	YES
	White Birch	11	0.51	0.30	YES
	White Birch	٣	0.50	0.47	YES YES
	Sugar Maple	3	0.55	0.85	YES
	Red Oak	7	0.80**	0.82**	NO NO

*p<0.05, ** p<0.01

TABLE 13

SAPSUCKER INJURY TO FEED TREES

SPECIES OF	NUMBER OF		BANDS			COLUMNS		BANDS & 1
FEED TREE	TREES	LIGHT	INTER.	HEAVY	LIGHT	INTER.	HEAVY	COLUMNS
Sugar Maple	67	8.2%	16.3%	28.6%	4.1%	8.2%	34.7%	0.0%
Red Maple	∞	12.0	75.0	12.0	0.0	0.0	0.0	0.0
White Birch	18	5.5	5.5	22.2	5.5	11.1	33.3	16.7
Basswood	7	0.0	0.0	100.0	0.0	0.0	0.0	0.0
Hemlock	5	0.0	0.0	0.0	0.0	0.0	0.0	100.0
Red Oak	6	0.0	0.0	100.0	0.0	0.0	0.0	0.0
American Elm	⊣	0.0	0.0	100.0	0.0	0.0	0.0	0.0
Yellow Birch	2	0.0	0.0	50.0	0.0	0.0	50.0	0.0
Balsam Fir	Н	0.0	0.0	0.0	0.0	0.0	0.0	100.0

 1 Only heavy injury.

TABLE 14

PRESENCE AND TYPE OF PREVIOUS DAMAGE TO SAPSUCKER FEED TREES

FEED TREE SPECIES	NUMBER WITH RECENT DAMAGE	PREVIOU SAPSUCKER	PREVIOUS DAMAGE KER NON-SAPSUCKER	NO PREVIOUS DAMAGE
Sugar Maple	29	19	9	7
White Birch	∞	7	0	Н
Basswood	င	Э	0	0
Hemlock	7	33	0	щ
Yellow Birch	Н	0	0	Н
Balsam Fir	Н	н	0	0
	}	1		1
Tota1	94	33	9	7
		(71.7%)	(13.1%)	(15.2%)

number of recently injured trees having previous sapsucker injury = number of recently injured trees without previous sapsucker injury) revealed that a significant number (P<0.005) of feed trees in current use had been previously damaged. Additionally, a significant (P<0.005) portion of those feed trees with previous damage had been damaged by sapsuckers.

Previous injuries to feed trees that were not caused by sapsuckers were most often caused by other woodpeckers. Trees in the MS and MSS areas often had pileated woodpecker (<u>Dryocopus pileatus</u>) excavations. The wood immediately surrounding these holes often would swell and these swellings were drilled by sapsuckers. Sapsuckers would also drill around nest or feed holes of other small woodpeckers.

Other injuries included broken branches, cankers, and other swellings. A favorite feed site would be the swelling around the stub of a broken branch. The sapsucker would often concentrate its drilling below such a branch. Cankers were also drilled frequently.

Feed trees were examined from the ground with regard to damage height in relation to the canopy to determine whether sapsuckers withdrew sap within or below the canopy. The results are presented in Table 15. A majority of the trees (67%) sustained damage below the canopy. Hemlocks are a special case as all sustained damage into their canopy. Branches of most conifers in mixed woods extend down the trunk farther and persist much longer than those of similarly aged deciduous species. The same remains true for the lone balsam fir measured, which sustained damage up into the canopy. Severe injury to trees was not extensive, as revealed by the number of feed trees (11%) that were dead or exhibited top dieback (necrosis of

limbs in upper parts of a tree, above the site of sapsucker injury.

TABLE 15

FEED TREES: RELATION OF DAMAGE TO CANOPY, SAPSUCKER INDUCED DEATH, AND TOP DIE-BACK

SPECIES	NUMBER OF TREES	IN CANOPY	BELOW CANOPY	DEAD OR DIE-BACK
Sugar Maple	49	2	47	3
Basswood	7	5	2	1
White Birch	18	6	12	5
Hemlock	5	5	0	0
Red Maple	8	5	3	2
Red Oak	9	9	0	0
Yellow Birch	2	0	2	0
Balsam Fir	1	1	0	0
American Elm	1	0	1	0
				
Total	100	33	67	11

The mean height of injury for each species in each study area was determined from the upper and lower limits of injury. A t-test was then used to determine if damage height differed for a species between areas and for two species within an area. The results are presented in Table 16. Only two tests indicated a significant difference in

damage height. Sugar maples at MS and MSS were damaged at a greater height than those at LB and PI and is most likely due to the canopy height being greater at MS-MSS. The other test, red maple versus sugar maple at LB, indicated red maples were damaged at a significantly greater height than the sugar maples.

TABLE 16

COMPARISON OF MEAN DAMAGE HEIGHT AMONG FEED TREE SPECIES AND STUDY AREAS

AREAS		SPECIES	NUMBER OF TREES	DF	t
MS MSS	vs.	Sugar Maple	48 34	80	0.45
PI LB	vs.	Sugar Maple	10 4	12	0.58
MS & MSS LB & PI	vs.	Sugar Maple	82 14	94	3.42**
MS MSS	vs.	Basswood	4 10	12	0.06
LB PI	vs.	White Birch	26 10	34	0.18
LB		Red Maple Sugar Maple ^{vs.}	16 4	18	3.13*
LB		Yellow Birch White Birch vs.	4 26	28	1.42

 $[*]_p < 0.01$

^{**}p < 0.001

of the 100 feed trees examined, 99 trees were in the top part of the forest canopy, that is, exposed to direct sunlight. Only one tree, at MSS, was overshadowed by its neighbors. Only three trees were obstructed by other trees within five feet (1.5 m) of the site of sapsucker injury. Two were located at MS and one at MSS; all were sugar maples. The lone balsam fir, at LB, while not crowded by the other trees, had branches which may have impeded sapsucker access. The hemlocks also had branches down their trunks but typically were branch-free at the site of injury. Additionally, injuries were located on that side which actually faced an opening in the forest. Whereas sapsucker holes may be found around the entire circumference of a tree, it is concentrated on the opening side. Sapsuckers had a clear fly-way to the feeding locations on the remaining trees.

Behavior

Observations of sapsucker behavior were made between 26 April and 18 July, 1973 and 1974. By the later date the young had fledged. Activity between 0645 and 1930 was recorded. Over 30 hours of sapsucker activity was observed.

Activity is divided into three categories: 1) interaction with other animals, 2) nest construction and 3) feeding. Interaction with other animals includes inter- and intraspecific encounters.

Sapsucker behavior I observed was a combination of visual (posture and activity) and audible signals. Activity, being more easily observed than posture, was emphasized. Sapsuckers had four main audible signals. 1) CRY-MEW. A call that starts hard and descends in both volume and scale. 2) CRY-YEEP. Similar to the

cry-mew but softer in the beginning and rising in scale at the end.

3) CRY-SCREAM. A loud, high-pitched squawk of short duration, as are the preceding two. 4) TATOO. A sequence of notes drummed out on a branch or trunk that is usually dead and highly resonant. It starts as a rapid series with increasingly longer intervals between raps. Other woodpeckers may tatoo, but do not slow down at the end.

Intraspecific Interactions

A full description and discussion of sapsucker behavior is not necessary for this paper and will, by and large, be avoided. Only selected types of behavior related to questions considered will be discussed.

Typically, nesting sapsuckers confront neighboring pairs through the tatoo. One bird will tatoo and the neighbor will answer, either with a tatoo of its own or with a cry-scream, rarely with a cry-mew. Tatoos are the main type of "communication" with other pairs for when territories were being established in the spring of 1974 near DUKE 1, three pairs of sapsuckers had a "tatoo duel" wherein 21 tatoos were rendered in a period of 3.5 minutes.

The likelihood of a sapsucker answering another sapsucker appears to be related to the frequency of border conflicts, i.e., how close the neighboring pairs are located. If other birds are nearby, more conflicts arise, the more readily a sapsucker will answer. This is illustrated by the birds at MS. The closest pair is located at some distance and few tatoos were exchanged between them. I imitated a tatoo every half-hour from 1130 until 1930 and recorded the immediate reply from the birds. The responses to my 17 tatoos were two tatoos,

one cry-scream, and one cry-mew. This would indicate that when border disputes are few, the birds are not "predisposed" to reply when challenged. This is further substantiated by the fact that few tatoos or audible signals of other types were exchanged by the MS pair with other pairs after borders were established in the spring.

Other evidence is provided by the number of birds in swamps, responding to tatoos. While investigating two very large and nearly impassable swamps at the Upper Peninsula Experimental Forest, I tatooed on any convenient log. Invariably, at least one sapsucker tatooed or cry-screamed in reply. In the swamp near DUKE 1, three or four birds answered back. This can most easily be attributed to more birds being present and their being more "predisposed" to reply.

Interspecific Interactions

Interspecific interactions were observed only between sapsuckers and other birds. Small birds such as red-breasted nuthatches (Sitta canadensis), myrtle warblers (Dendroica coronata coronata), and ruby-throated hummingbirds (Archilochus colubris) were frequently encountered. These typically occurred at feed trees and the sapsucker either ignored the others or shifted around the tree, away from the other birds.

Interaction with a large bird was observed only once, that was when a crow (Corvus brachyrhynchos brachyrhynchos) flew over a feeding sapsucker. The sapsucker's attention shifted immediately to the sky.

This may indicate an extreme "wariness" to crows, possibly because they may be predators.

Hummingbirds may have a special relationship with sapsuckers.

Once a ruby-throated hummingbird followed a sapsucker to the latter's nest tree. The ruby-throat remained a few minutes after the sapsucker entered, then flew off. The other encounter observed is quite intriguing. Once while looking for sapsuckers, I imitated the tatoo. When no reply was received, I imitated the sound of a sapsucker drilling feed holes. Within a few minutes a ruby-throated humming-bird was flying around the tree T was rapping. After a few moments it disappeared as quickly as it had appeared. This seems to indicate that hummingbirds can recognize the sound of a sapsucker drilling and the possibility of food becoming available.

The other interaction frequently observed was with hairy woodpeckers (<u>Dendrocopus villosus</u>). In a one-on-one encounter, the sapsucker would invariably give ground, with much vocalization (cryscream). This apparent inability to co-habit a section of wood with
hairy woodpeckers is further supported by the following observation.
A pair of sapsuckers appeared to have a nest when a hairy woodpecker
entered the area. There was much vocalization between them but the
hairy woodpecker remained. Within a few days the sapsuckers abandoned
the tree and were not found on subsequent visits to the area.

The only time a hairy woodpecker was driven out of an area was when three sapsuckers of undetermined sex gave chase. Actual contact was made between antagonists before the hairy woodpecker left.

Nest Construction

The male and female work on nest excavation on a rotational basis. The sapsuckers typically vocalize as they change places.

An example will illustrate. On 8 June 1974, the male landed by the nest entrance and cry-yeeped three times. The female emerged from the nest and flew to a nearby tree. The male then entered. A cry-yeep is not always given, however. On one occasion the male left with a "rattle-wiffle," similar to the "rattle-cry" of Howell (1952). The female then entered, in silence, and started excavating.

The time spent inside the developing nest cavity varied greatly. An individual may stay from five to twenty minutes. The birds are not audibly drilling the entire time they are inside. Upon reemerging, the sapsucker often carries sawdust in its bill. It flies to a nearby tree, almost always the same one. There the sawdust is dropped and the bird preens. It then often captures an insect or two or laps some sap before returning to work. The entrance is always so small that whenever entering, the adult sapsucker has to wriggle to get inside.

Feeding

Sapsuckers have two main sources of food: sap-bast and insects. Insects are extremely important for the sapsucker cannot survive on sap and bast alone (Bolles, 1892).

Drilling for Sap and Bast. The sapsucker typically drills new holes above old holes (Bolles, 1891). One female on a hemlock at DUKE 1 added a new hole to each column of holes. Periodically she would drop down the trunk, approximately eight feet (2.5 m), drill a few holes and then hitch back up the tree and continue to add new holes at the top of the others.

On one occasion a male was observed to fly from tree to tree, stopping at each and drilling a single hole. The holes were not drilled at the same height or facing the same direction. Most of the trees were in the immediate vicinity of the nest tree.

Sapsuckers were seldom seen on small trees. The birds had difficulty climbing on such trunks because of the smooth bark. On a young sugar maple I watched a bird trying to hitch up the trunk, but it continually lost its grip.

Insects. Insect capture is of two types. In the first, the bird typically works its way up the tree trunk or branch, picking insects off the bottom of leaves or from the bark. Often the birds were seen to pound at the bark plates to dislodge them to gather insects. I never observed a bird to randomly fly against the foliage when gathering insects. The sapsuckers collect individual insects that are easily discernible, mostly because they are backlit and appear as dark spots on the translucent leaves. A sapsucker often works a tree over very thoroughly. After traveling up into the foliage it will fold its wings and drop, flare its wings and land on the trunk, then hitch up the tree again.

The other method of insect capture was observed first at a dead tree located in the middle of the beaver ponds at DUKE 1. The sapsucker would sit on the dead tree until a large flying insect was observed (also visible to this investigator without the aid of binoculars). The bird would then fly out the two or three meters and capture the insect, fly back to the tree and pound the insect against the tree. The insect was often not captured on the straight fly but would be chased, the sapsucker being extremely agile, in a

manner reminiscent of a flycatcher. An average of three insects (range 2 to 5) were captured before the sapsucker returned to the nest to feed its young. The birds always stopped first at a feed tree before presenting the food to the young.

The time between trips to feed the young was recorded at DUKE 1, MS, and M-94. The flycatcher method of insect capture was used at DUKE 1 whereas foliage capture was used at MS and M-94. The average time between nestling feedings at DUKE 1 was 2.5 minutes, 2.2 minutes at MS, and 5.4 minutes at M-94. The sapsuckers at M-94 had to fly at least 400 meters to gather insects. Few captures occurred in the immediate area of the nest, perhaps because of the tightness of the canopy. In fact, the birds used the old logging road as a fly-way, leaving it only when opposite the nest. Sapsuckers feeding on sap were seen to interrupt their activity to capture nearby insects. Typically, as an insect comes to the attention of the sapsucker, the bird will follow the insect's activity (flight) with its bill. If the insect comes close enough, a capture will be made without the bird leaving the tree.

In the early spring other food sources are utilized. On 26 April, a sapsucker was observed to alternate between sap and bast from maples and birches to catkins of quaking aspen.

DISCUSSION

Nest Trees

The nest tree measurements coincide with those described by other investigators (e.g., Bolles, 1891; Howell, 1952; Kilham, 1962; Tatschl, 1967; Bent, 1939). The minimum diameter of 6.3 inches (16.0 cm) is noteworthy in that this is most likely related to the internal dimensions of the sapsucker nest. Trees with trunks or side branches with a smaller diameter will most likely not be utilized by sapsuckers. This may be another reason why sapsuckers were unsuccessful at nesting in Kilham's (1969) study area. The small variability of nest entrance diameter is expected since the holes are only just large enough to allow the passage of an adult and adults should vary little in size. A larger diameter hole is probably avoided to reduce the incidence of nest raiding by predators (raccoons and weasels; Johnson, 1947).

Nest height was quite variable (Table 1). However, nest height appears to be correlated with that portion of the tree in which the nest is located. The mean heights were 17.0 ft. (5.2 m), 29.8 ft. (9.1 m), and 51.6 ft. (15.7 m) for stub, trunk and branch nests, respectively. These results are expected since stubs were the shortest structures that were used for nesting, trunks next in height while branches on living trees were tallest. The relatively equal frequencies with which these heights were used (3:2:3) appears to indicate no advantage connected with any particular height.

It was originally thought that nest entrance headings may be clumped to take advantage of solar radiation, for heating or illumination of the nest cavity. One would then expect one heading, say south, to predominate. The clumping exhibited, in opposite directions, does not appear to support this hypothesis. Conner (1975) has suggested that sapsuckers locate their nest entrance on that part of the bole that faces the ground. Sapsuckers supposedly take advantage of the fact that most trees are not normal to the ground, that is, are at some angle to it. By locating their nest entrance on that part facing the ground some shelter from the weather is gained. Since the angle of the nest entrance above and below the horizon was not measured, this hypothesis could not be tested.

Nest tree condition (Table 2) was examined to determine if trends exist that may define the sapsucker's "search image" of a nest tree. The condition of the entire tree is not as important as the condition of the tree section where the nest is located. All nest sites examined were dead whether in stub, trunk, or branch.

Kilham (1971) stressed rather strongly the fact that sapsuckers nested in poplars with heart rot caused by Fomes igniarius, even though 21 of 25 nests were in stubs or dead portions of trees. Sapsuckers nest in dead portions or those with heart rot because the wood is more easily excavated. It therefore appears that two important characteristics of a nest tree are a minimum diameter of 6.3 inches (16.0 cm) and easily excavated wood (e.g., dead or with heart rot). If there are no trees with these characteristics, the sapsucker should not nest. This was demonstrated beautifully in the section of trees that Kilham (1969) studied. As the trees that had been nested in

were replaced by young trees, too small in diameter and offering no dead wood, sapsuckers were unsuccessful in finding a nesting site.

Interestingly, the same problem existed for the hairy woodpeckers of that area.

How does a sapsucker identify a dead tree or one with heart rot? It could go around and test every tree or branch but this is highly unlikely. Visual cues (search image) seem most appropriate and may include the lack of bark or presence of conks, in the case of heart rot. The former may be a sufficient but not a necessary cue, since only five of the nests I examined lacked bark. The lack of bark may have another benefit by discouraging predators. Johnson (1947) observed a weasel trying to prey upon a sapsucker nest. The weasel was unsuccessful because it could not cross the barkless region below the nest entrance.

Another feature of nest trees mentioned often is the presence of openings in the forest around the nest tree. These openings may also influence the direction of the nest opening, i.e., the nest entrance hole facing the free space. For instance, Philipp (1917) described the favored tree as often being on a stream bank with the nest opening facing the stream. Erskine (1972) found the birds preferred rotten stubs in recently logged areas. I examined "openness" of the nest by measuring the distance of the canopy i.e. from the nest at nest height and comparing this distance with the canopy distance around the rest of the tree. The results were inconclusive. Only one test was significant, with the distance to the canopy being significantly greater at the nest than at the other angles around the tree. An examination of the data, however, reveals that only two trees had less than 6.4 feet

(2 m) clear space in front of the nest entrance. The hypothesis of canopy openness was also examined by considering if the pairs could fly above the canopy after leaving the nest without having to pass through the canopy. The MS nest is not considered with the other trees since the nest was located completely below the lowest margin of the canopy. At MS the forest lacked any undergrowth of shrubs or saplings and therefore was quite open. All flights of this pair of sapsuckers took place in this clear space. This means that 76% of the nests examined had at least 6.4 feet (2 m) clear air at the nest entrance. If clear air space is necessary, the minimum distance necessary may be less than that observed. Additionally, openings were looked at by examining the surrounding trees (Table 4). The results confirmed visual impressions. The significant tests (DUKE 1 and YD) were at nests where the nest tree was the solitary occupant of a clearing.

What advantage is there in clear air space at the nest? Five possibilities present themselves. 1) There is no advantage. Openings are a consequence of that part of the tree being dead. Dead trees lose leaves and limbs, thus automatically creating openings in the canopy. The sapsucker does not chose a tree with little canopy around it, but dead trees frequently are isolated just because they are dead. 2) Predator protection. If the nest tree is separated from those surrounding it, predators will not be able to jump from one to the other. Johnson (1947) saw this occur when a weasel attempted to enter a sapsucker nest. After repeated failure in climbing the nest tree the weasel climbed neighboring trees and attempted to jump across. The distance was too great and the assault was soon

stopped. This has also been suggested as a reason why Williamson's sapsucker (S. thyroideus) nests in tall pines (Crockett and Hadow, (1975). 3) Sapsuckers may nest in trees that are near their feed trees. Feed trees may be located in open woods (see Feed Trees) and nearby nest trees will also be in open woods. Again, the bird is not selecting for trees in openings, but openness is coincidentally associated with those they select. Crockett and Hadow (1975) came to this conclusion with regard to Williamson's sapsucker, stating " . . . nest sites were chosen for their proximity to suitable foraging habitat rather than on the characteristics of the aspen nest stand itself." The last two possibilties involve aspects of the sapsucker's behavior. 4) Reduced energy demand. Although the bird is extremely agile and quick in flight, a clear fly-way to the nest would require less energy, thus reducing its energy demand. Sapsuckers nest in trees in openings because they are easier to reach. 5) Sapsuckers nest in trees that look like their feed trees. This means the search image for nest and feed trees could be very similar. The bird is attracted to isolated trees. If it is alive, it may be drilled for food and if dead, drilled for a nest.

The first and last two are most likely, especially those dealing with behavior. Nests were often located along logging roads (Table 5). At M-94 the sapsuckers regularly used this clear road as a fly-way. Although flight was regularly done within the canopy, the road was used when traveling to the swamp. Flight through unobstructed air requires less vigilance (in locating obstacles) and energy (in avoiding obstacles). Besides requiring less energy to reach, locating in the open may mean increased solar radiation reaching the

nest. This may provide heating sufficient to free both adults for foraging.

Feed Trees

The nine species of tree used by sapsuckers in obtaining sap and bast have been encountered by previous investigators (e.g., Kilham, 1953; Rushmore, 1969; Tate, 1973). Deciduous trees were used most frequently although hemlock and balsam fir were also drilled.

The feed tree areas were first examined to determine if the sapsuckers selected only one size of tree. Feed trees from adjoining areas were similar in size, i.e., feed trees from MS and MSS were not significantly different in size. This is to be expected since both areas have been subjected to the same management practices. Interestingly enough, the feed trees from the remaining two areas were also similar in size. This is especially surprising when one considers those trees at LB are unmanaged whereas those at PI are located in a park-picnic ground. The similarity in tree size at PI and LB is considered coincidental. These tests reveal that the sapsucker is not limited to an area because of tree size, but that those trees available are the ones that are utilized. Four inches DBH (10.2 cm) was arbitrarily picked as the lower limit for measuring trees. All trees in each study plot were examined and only one tree less than four inches DBH was found to have sapsucker feed holes, although Erdmann (personal communication) has found sapsucker damage on saplings down to 2.1 in. (5.3 cm.).

The apparent selection of larger trees may be related to the amount of sap available to the bird. Since sap production is

related to photosynthetic rate, the higher the rate of photosynthesis the greater the sap flow. Assuming equal availability of water and nutrients, the more light a plants gets the greater its photosynthetic rate (Foster, 1966). Those trees which are smaller will be overshadowed by larger trees and should have a lower sap flow. This appears to be the case with sapsucker feed trees. All the trees but one were in the top part of the canopy. The sapsuckers are therefore tapping into those trees that should have the highest sap flow. It should be noted that sapsuckers have also been observed to utilize smaller plants (Woodburn, 1938). For instance, Howell (1952) saw sapsuckers on small willows along a creek. Since many creeks are not overgrown but are open to the sky, such willows are not necessarily overshadowed and could carry on a high rate of photosynthesis.

Feed trees of the same species were more often of similar size than not, even if they were found in two different areas (Table 9). Differences, where they occurred, were most likely not due to selection on the part of the sapsucker. The two cases in point are basswood at MS and MSS plus sugar maple at PI and MS-MSS. Smaller sugar maples were used at PI because all the trees at that area are smaller than trees at MS-MSS. In other words the sapsucker utilizes those trees that are available to it and size, above some minimum, is not that critical. The difference between basswoods at MS and MSS may be less real than the statistics indicate. I say this because first, the t-test is based upon a small sample size (n=7) and second, the other feed trees are very similar in size. This is borne out by a further examination of the feed trees.

The size of the feed trees, based upon the basal area, does not necessarily change with the species of feed tree within a study area. Seven of the eleven comparisons (Table 10) that were possible indicated no difference in basal area of the feed tree species in a particular study area. Factors other than sapsucker selection are probably responsible for three of the significant tests. White and yellow birch were larger than red maple at LB. This is most likely due to the fact that shade tolerant red maple is filling in some spaces as the white birch matures and dies. The red maple is being utilized as soon as it is large enough, even though it is still much smaller than the birches it is replacing. Secondly, red oaks were larger than sugar maples at PI, a circumstance due mostly to the action of man. The species composition of this area is controlled through the selective cutting and maintaining of trees by man. Red oaks were the dominate trees when the picnic area at Presque Isle Park was established. The size differences of tree species is due to man's action, not sapsucker selection. Lastly, the difference in size between white and yellow birch at LB may be due to a bias in the sample. Many of the white birch came from a small cluster which at one point constituted a feeding orchard (Tate, 1973). Most of the trees are now dead, because of sapsucker activity, although a few are still being used.

But how do feed and non-feed trees of the same species in the same area compare? The results in Table 11 are quite revealing. In ten of the twelve comparisons (83%) the feed trees were larger than the non-feed trees, although only four t-tests were significant. Sapsuckers may prefer larger trees because 1) the trees offer a

"better" sap source, either a larger sap flow or a better "quality" sap and 2) the sap at these trees is more easily harvested. I believe it is a combination of both. Sap flow, as already stated, is often related to the amount of photosynthesis taking place. A larger, more mature tree should be at the top of the canopy and therefore exposed to more sunlight. Besides producing a larger sap flow, the sap may be "better" for the sapsucker either because it is more concentrated or contains more nitrogen. Unfortunately, very little work (Tate, 1973) has been done on sap quality of sapsucker feed trees.

The number of trees in an area does not appear to influence the density of sapsuckers nesting in that area. If the two factors were related, the percentage of injured trees should stay the same or increase as tree density increases. In either case, the two should be coupled. A regression analysis of feed tree number indicates that the frequency of sapsucker injury is not related to the density of trees, at least in the areas studied. The positive results for red oak at PI is probably not significant for two reasons: 1) the stand of trees is artificially maintained and 2) is used by transient birds, not nesting pairs. The other significant test, basswood at MSS, is quite interesting. In this case, however, it is believed to indicate nothing more than a strong preference for basswood sap. Since only 28% of the trees examined at MSS were basswood, their total contribution to the food supply is not that great. The main feed tree species, sugar maple (77%), showed a very low r value (0.10 to 0.14). These results seem to indicate that territory size is based upon some other criterion, at least in the areas studied. This does

not preclude, however, some lower limit, some minimum number of trees that must be present before sapsuckers nest.

The number of different species of feed trees utilized is related to how many different species are available. Thus, sapsuckers appear to be opportunistic. This is supported by the fact that 285 species of woody plants have been used by sapsuckers (Shigo, 1963). As the diversity of the study areas increased, a larger variety of tree species were used. However, this does not appear to influence the densities of sapsuckers. Such flexibility on the sapsucker's part allows it to inhabit not only many areas throughout the United States but also the same section of woods as succession occurs.

One of the most significant characteristics observed on feed trees was the presence of previous injury. These injuries were most often related to sapsucker activity. Oliver (1968) also noted this and related that only 7 of 38 freshly drilled trees were injured for the first time. In addition to utilizing trees that had been used in previous years, drilling was directed at locations exhibiting injuries of other types. These include the work of other woodpeckers and injuries due to the loss of tree limbs. This type of selection is probably quite advantageous from an energy standpoint. Drilling must require tremendous amounts of energy. By drilling at places that previously yielded sufficient food supplies (sap), the probability of again obtaining food is high or at least higher than expected through random tapping on trees. In addition, sapsuckers tend to concentrate their effort on parts of trees that would have a higher sap flow, such as the swellings around other woodpecker damage or broken tree limbs.

The number of trees dying because of sapsucker injury was very small. Only 11% of those examined were dead or exhibited top dieback. Half of these trees (n=5) were white birch, mostly from an old feeding orchard at LB. These mortality rates are much lower than those reported by others. Tate (1973) recorded a loss of 2 to 5 trees per year out of feeding orchards. Rushmore (1969) reported mortality rates of 1% for hemlock, 40% for red maple, 51% for paper birch, and 67% for gray birch in ten territories. It is interesting to note that my mortality-dieback value is the same as that arrived at by Erdmann and Oberg (1974).

Most trees were injured below the canopy, that is, below all the photosynthetic organs. In this way all photosynthetic products are potentially available for exploitation. If this is true, differences in canopy height would account for the differences in sapsucker injury height among the areas studied. The exceptions found (Table 16) are related to the differences in the size of trees compared. The sugar maples at MS and MSS were larger (basal area) than those at LB and PI. Since basal area and tree height are positively related, the larger trees have their canopy at a greater height. They are injured at a greater height. Red and sugar maples at LB were not consistent with this pattern. Even though red maple was smaller, it sustained injuries at a greater height. No explanations present themselves.

Factors that influence sap production in trees most likely determine the "attractiveness" of that tree to sapsuckers. As already mentioned, solar radiation reaching the tree is very important.

Trees with more of their crown exposed should photosynthesize more

and should be more prone to sapsucker exploitation. Such appears to be the case, at least for yellow birch. Erdmann and Oberg (1974), in attempting to promote growth of yellow birch, subjected selected trees to varying amounts of crown release. This treatment removes the surrounding trees, exposing the canopy to more of the sun's rays. The results were startling. While control trees (those without any crown release) were used only 7% of the time by sapsuckers, 40% to 67% of the trees receiving the heavy crown release treatment (where all trees whose crown were within 15 feet of the selected tree's crown were cut) were utilized by sapsuckers.

Sapsuckers were obviously able to distinguish between trees, either visually or after sampling sap. The difference in the quality of sap, or in ease of exploitation, was sufficient to offset the energy spent in exploiting this food source.

One other environmental factor influencing photosynthesis is water stress. Photosynthetic rate is related to CO₂ concentration inside the stomata. The degree to which stomata are open determines this CO₂ concentration. If the stomata are closed, CO₂ concentrations decrease until the compensation point. The degree to which stomata are open depends upon the amount of water stress the plant is subjected to. In addition, the temperature of leaves influences net photosynthesis. The temperature of leaves is regulated to a large extent through transpiration. If a plant is allowed to transpire freely when leaf temperatures increase, the leaves are cooled, resulting in higher net photosynthetic rates (Hofstra and Hensketh, 1969). Transpiration rate is determined by water stress. At low water stress, the stomata open more as the temperature increases.

With increasing water stress, stomata close as temperature increases. The transpirational cooling lowers leaf temperature to a more favorable range for photosynthesis (Schulze, et al, 1973). Thus trees with adequate water will be able to transpire, to sustain a higher net photosynthetic rate during the heat of summer. These trees should have a higher sap flow and possibly different quality sap. Sapsuckers appear to be able to distinguish differences in sap quality and would be expected to select and exploit such a food source.

The literature is replete with examples. Aldrich (1934) mentions sapsuckers living in a yellow birch swamp forest. Bendire (1888) maintains they prefer nest trees near water. Bolles (1891) found feeding orchards in swamps and river delta. Erskin (1972) states they frequent aspen groves within site of water. Kilham (1956, 1958, 1971) mentions feed trees on or bordering swamps and streams. Reece's bog, studied by Tate (1973), had nine active territories and six feeding orchards. But the best example was provided by Rushmore (1969). He relates that in dry summers, some red maples on the edge of marshy ground were used more often and longer than nearby red maples on higher, drier ground.

Data collected in this study also provides substantiating evidence. Water of some type was found at all nine study areas (Table 6). These ranged from streams to pond, lakes, and swamps.

There is an additional advantage to sapsuckers by locating near water. Aquatic systems provide an excellent breeding place for insects. It would present to the birds a whole new group of insects to be exploited. Sapsuckers at DUKE 1 and YD were observed

to regularly hunt insects at these water sources. Other investigators, such as Philipp (1917), Hicks (1933) and Bent (1939), have reported a preference for nesting near water.

This may be why sapsucker density appears to be greater in swamps. Trees living there can always be relied upon to provide sufficient amounts of sap. Additionally, insect numbers should be quite high. When searching for sapsuckers I would invariably receive replies from two or three birds whenever I tatooed near a swamp.

<u>Proposed Territorial-Habitat Requirements</u> and Hypothetical Selection Mechanisms

Although sapsuckers often renest in the same tree, eventually such a tree will be so riddled with holes it can no longer stand.

The DUKE 1 and YD trees are prime examples. How do sapsuckers select another nest tree? What criterion must the tree meet and what "clues" are used by the sapsucker?

In most woods there are sufficient numbers of dead trees or dead limbs from which a selection can be made. "Deadness" is most likely determined visually, possibly by the lack of bark, leaves or twigs. If dead boles are not available, those with heart rot may be recognized by conks. The selection may also be aimed at other sapsucker or woodpecker holes. Since sapsuckers appear to start three or four holes before settling upon the final one, pairs could select trees already worked upon. Another facet of the search image may be isolation from other trees, at least on one side. This would include trees located along streams or on the edges of lakes, areas which, incidentally, provide excellent feed trees.

All of these are visual cues and can be assessed from a distance. The birds do not have to come into actual contact with the tree. Since tree selection usually commences before much leafing out has occurred, the visual signals such as "Total Deadness," "Stub" (total lack of branches), or "Barkless" may be most important.

"Heart Rot" (presence of conks) may be another.

Selection of this sort must occur, otherwise too much energy would be spent by flying around and randomly sampling every tree and branch. Then the selected tree or branch must meet minimum requirements with regard to diameter, straightness, and tilt of the bole. How the diameter is measured is not known. The birds may possess enough visual acuity to enable it to "measure by eyeball." Or it may determine bole size by climbing upon it. If measurement is made through physical contact, straightness of bole and tilt can also be assessed. If the selected site is satisfactory, location of the nest entrance would be determined and construction started. If the wood is too hard or too soft, the hole could be abandoned and another one started.

The presence of water may also influence the selection of an area. This may not be an absolute necessity, although very desirable. If it does influence selection, the presence of water is most easily assessed in the early spring when the birds arrive and before leafing out of the trees has occurred. The early hatching of some aquatic insects may also notify the birds that water is nearby.

Continued use of a feed tree often results in death of that tree. New ones must continually be exploited. How are these trees selected? What is the search image the sapsucker uses? The selection

process probably starts by remote sensing, that is, when the bird is not in physical contact with the tree. This most likely involves the rejection of tree species that provide "poor" sap while selecting for species with "good" sap. Sapsuckers tend to reject conifers and select deciduous species for summer feed trees. The presence or absence of leaves would indicate those individuals that are living or dead. Now that the selection is down to living deciduous trees, which ones will be drilled?

There appears to be selection for trees having a minimum diameter. Once again the birds may be able to visually determine if the tree is large enough (basal area) or in the top part of the canopy. Such selection, however, may be done once the bird is in contact with the tree. Small trees often have smooth bark. Since sapsuckers have difficulty getting a grip on such trees, they would be avoided.

Older (larger) trees with bark plates would be more easily climbed and drilled and would be used more.

An examination for injuries may occur next. Clues could include swellings, missing bark, streaming sap, or discoloration. Another may be isolation from other trees. All of these may be sufficient releasers and result in feed holes being drilled. Conks have been suggested by others as such releasers for nest construction. An observation by Oliver (1968) may help to illustrate. An open-grown ponderosa pine had extruded sap in a crescent pattern just below some of the larger branches. Each series was diligently duplicated by a small crescent of sapsucker feed holes.

Use of these criterion by the sapsucker would result in only injured trees being drilled. Yet many feed trees have no other

injuries. Satellite bands have been suggested as one way healthy trees are first drilled. Sapsuckers drill a single band of holes on trees adjacent to main feed trees. This type of behavior may be very advantageous since those factors that influence sap production (water stress, nutrient availability and sunlight) are most likely to be the same for the satellite tree as for the feed tree. This may be the way feeding orchards are established. I also observed another way new holes are established. Sapsuckers may go around and drill one or two holes into trees. If sap production is sufficient, sap should stream from the holes. As already stated, sap on a trunk is a sufficient releaser to cause more holes to be drilled. But not all trees that are drilled are used. Only a few trees provide most of the sap used by a nesting pair. Those trees that prove to have an insufficient sap flow or "poor" quality sap are abandoned.

Since the birds arrive in early spring, before most trees have leafed out, how are feed trees selected for immediate use? Sapsuckers usually select trees with sap flow. Selection of conifers, particularly hemlocks, which are photosynthesizing, would be a relatively easy process since they are one of the few trees in the deciduous forest which have leaves at that time. Previous sapsucker injury or fungal infections on maples may also make flowing sap visible on the bark of affected trees.

It appears that those characteristics that make a good lumber tree also attract sapsuckers. Sapsuckers may be prevented from nesting in an area by removing all the trees that are suitable for nest excavations (e.g., dead limbs). This would not eliminate the damage caused by transient birds, however. The effect of removing these trees goes beyond the sapsucker and may affect the populations of other birds and animals. The gains and losses to be incurred through management practices have to be assessed before such steps are initiated.

CONCLUSIONS

- Sapsuckers prefer nesting in dead portions of trees, either stub, trunk, or branch.
- 2. The minimum diameter of the bole at nest sites was 6.3 inches (16.0 cm) and is most likely related to the size of the sapsucker nest cavity.
- 3. Nest height was quite variable and does not appear to be critical to the sapsucker.
- 4. Nest entrance headings appeared to be clumped in NE and SW directions.
- 5. Eight of nine nests studied had at least 6.4 feet (2 m) clear space at the nest entrance.
- 6. Surface water was present in all nine territories studied.
- 7. Trees down to 4 inches (10.2 cm.) DBH may be drilled for sap by sapsuckers.
- 8. Sapsuckers utilize any species of deciduous tree to obtain sap, as long as sufficient sap flow is present and it can be exploited easily.
- 9. Tree mortality caused by sapsuckers is low in this study compared with that reported in other areas. The amount of damage caused, however, was not assessed.
- 10. Trees fed upon by sapsuckers tend to be larger than those not fed upon, possibly because of higher photosynthetic rates in larger trees.

- 11. Sapsucker density does not appear to be influenced by tree density. A minimum density, however, is undoubtedly required before successful nesting can occur.
- 12. More species of trees are utilized as food sources as the diversity of the forest increases.
- 13. Previous damage (sapsucker or other) is a very strong attractant to the birds. An injured tree has a greater chance of suffering sapsucker injury than an uninjured tree.
- 14. Those trees considered "good" by foresters are also considered "good" by the sapsucker.
- 15. Management of sapsuckers should be approached through control of their nesting sites. Elimination of suitable nest trees will prevent reproduction and reduce sap demands. Care must be taken, however, so that other animals that utilize sapsucker excavations are not adversely affected.

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 $\label{eq:APPENDIX 1} \mbox{$Basal$ area (m^2/ha) of tree species found at each nest tree.}$

			Nest Tree	e	
Tree Species	MS	MSS	OT	DUKE 1	CURVE
Sugar Maple (Acer saccharum)	35.977	34.998	31.614	26.953	28.916
Red Maple (Acer rubrum)					3.164
American Elm (<u>Ulmus</u> <u>americana</u>)		0.492		1.059	0.281
American Beech (Fagus grandifolia)		0.212	0.208		
Yellow Birch (Betula alleghaniensis)		1.587		0.471	1.369
White Birch (<u>Betula papyrifera</u>)					
Basswood (<u>Tilia</u> <u>americana</u>)		0.602	0.106	1.183	
Balsam Fir (Abies balsamea)					0.544
White Spruce (<u>Picea glauca</u>)					
Black Spruce (<u>Picea mariana</u>)					
Hemlock (<u>Tsuga</u> <u>canadensis</u>)					1.766
Cedar (<u>Thuja</u> <u>occidentalis</u>)					
Unidentified					
Total basal area at each nest tree (m²/ha)	35.977	37.897	31.929	29.668	36.043

APPENDIX 1 (continued)

Basal area (m^2/ha) of tree species found at each nest tree.

Nest Tree

		HUBL	1166	
	M-94	YD	LB	HMC
Sugar Maple (<u>Acer saccharum</u>)	2.915	18.804	0.563	1.679
Red Maple (Acer rubrum)	7.056	0.169	8.171	
American Elm (<u>Ulmus americana</u>)	0.292			2.484
American Beech (Fagus grandifolia)				
Yellow Birch (Betula alleghaniensis)	15.264	4.362	2.251	
White Birch (<u>Betula papyrifera</u>)			10.386	6.016
Basswood (<u>Tilia</u> <u>americana</u>)				
Balsam Fir (<u>Abies</u> <u>balsamea</u>)			7.198	0.669
White Spruce (<u>Picea glauca</u>)			3.288	
Black Spruce (<u>Picea</u> <u>mariana</u>)			1.459	
Hemlock (<u>Tsuga</u> <u>canadensis</u>)	1.341	5.348		0.808
Cedar (<u>Thuja</u> <u>occidentalis</u>)		1.012		
Unidentified				11.731
Total basal area at each nest tree (m²/ha)	26.870	29.696	33.319	23.389