

USE AND SELECTION OF SAP TREES BY YELLOW-BELLIED SAPSUCKERS

LAURIE S. EBERHARDT¹

Department of Zoology, University of Florida, Gainesville, Florida 32611, USA

ABSTRACT.—Yellow-bellied Sapsuckers (*Sphyrapicus varius*) obtain phloem sap from clusters of holes that they peck in living trees. I examined trees that sapsuckers used for sap extraction in northern Michigan and tested several hypotheses to explain why they choose specific trees for attack and why they cluster their holes in one place on the bole of each of these focal trees. Sapsuckers preferentially attacked individuals of paper birch (*Betula papyrifera*), red maple (*Acer rubrum*), juneberry (*Amelanchier* sp.) and bigtooth aspen (*Populus grandidentata*). They made clusters of sap holes an average of 7.13 m from the ground and within 1 m of a live branch; most clusters were located above old holes or other wounds from previous years. Each new sap incision through the bark to the phloem stream was made above a previous one and was enlarged for an average of 3.1 days before being abandoned for a new, higher hole. The resulting long vertical chains of holes were made alongside others to form tight clusters of holes at a single spot on the tree. Sapsuckers did not select trees for sap extraction based on location relative to nesting sites or on microclimate conditions of water availability and tree density. Individual trees used for sap extraction did not have thinner bark, more moisture in bark samples, or larger crowns, but they did score lower in an index of overall tree health. Experimental evidence suggested that sapsuckers cluster their holes to induce the accumulation of sap in bark that they will attack for future sap extraction. Thus, sapsuckers appear to overcome some of the difficulties in obtaining phloem sap by choosing specific species and individuals, clustering sap holes above previous wounds, and possibly by farming their resource throughout the season by girdling the tree's phloem stream with each successive sap incision. I attempted to duplicate the wounding techniques and patterns of wounding of sapsuckers but was unable to induce sap flow from the same or similar trees in the area. Received 10 August 1998, accepted 27 April 1999.

NORTH AMERICAN SAPSUCKERS (genus *Sphyrapicus*) mine sap by building sap wells made up of clusters of holes in the bark of trees (Tate 1973). These unique feeding places yield copious amounts of sap and provide feeding sites not only for the sapsuckers but also for a whole suite of animals that steal sap from the wells (Foster and Tate 1966, Daily et al. 1993). Although numerous papers have described these sap wells (e.g. Kilham 1964, Lawrence 1967, Tate 1973), why sapsuckers make large sap wells in single places on trees rather than scattering their holes on many trees throughout their territories has not been examined experimentally. In addition, exactly how sapsuckers obtain sap from their holes remains unknown.

Sapsuckers feed on both xylem and phloem sap of trees during different parts of the year (Tate 1973). Here, I focus only on the problem

of getting phloem sap because it is their main source of sap during the breeding season. Phloem sap travels through chains of living sieve cells. Between each sieve cell lies a sieve plate with small pores (Salisbury and Ross 1992). Sap passes through the sieve pores when intact, but upon injury, sap flow is arrested as a result of collapse or clogging of the cells by proteins and carbohydrates (Kallarackal and Milburn 1983). When coupled with a thick layer of cuticle or bark, the self-sealing mechanisms of sieve cells apparently protect phloem sap from most herbivores (Crafts and Crisp 1971). Sapsuckers obtain phloem sap by making incisions into the stream of phloem sap and must overcome the plant's self-sealing mechanisms in the process.

Relatively little is known about how vertebrates mine phloem sap. Several types of primates (Coimbra-Filho and Mittermeier 1976, Charles-Dominique and Petter 1980, Rylands and de Faria 1993, Soini 1993) and gray squirrels (*Sciurus vulgaris*; Kenward 1982) strip or

¹ Present address: Department of Biology, Valparaiso University, Valparaiso, Indiana 45383, USA. E-mail: laurie.eberhardt@valpo.edu

make holes in bark and may get phloem sap, although the bark itself and plant secondary exudates like gum and resin may be the main food they obtain from this behavior. The Yellow-bellied glider (*Petaurus australis*) is the only mammal besides humans that clearly is known to extract phloem sap from trees. These gliders cut V-shaped grooves into boles of some eucalyptus species. They choose individual trees for attack (Henry and Craig 1984, Mackowski 1988, Goldingay 1991), possibly those with poor sap-defense properties. They also make repeated cuts into fresh tissue above the old wounds (Goldingay 1987) and may be able to obtain sap simply by bypassing clogged tissue. In addition, gliders may use saliva (Mackowski 1988) as a way to remove protein and carbohydrate blockages of severed phloem tissue. Birds that have been observed to make incisions for sap include the North American sapsuckers (Tate 1973, Daily et al. 1993) and other woodpeckers including Acorn Woodpecker (*Melanerpes formicivorus*; MacRoberts 1970, MacRoberts and MacRoberts 1976, Kattan 1988), White-fronted Woodpecker (*Melanerpes cactorum*; Genise et al. 1993), and various European and Asian species (White 1873, Zusi and Marshall 1970, Gibbs 1983, Ripley 1989). As with most of the mammals, little is known about how these woodpeckers overcome plant defenses to obtain sap from the holes they construct. What is clear, however, is that phloem sap is difficult to obtain through bark incision, and relatively few animals are able to exploit sap in this manner.

The Yellow-bellied Sapsucker (*Sphyrapicus varius*) is the most migratory and widespread of the sapsuckers (Howell 1953). These sapsuckers use a variety of tree species for sap collection on both the wintering and the breeding grounds (Rushmore 1969, Tate 1973). However, during the breeding season, both Kilham (1964) and Tate (1973) found that Yellow-bellied Sapsuckers focus all sap collecting activities on only a few individual trees of mostly birch (*Betula*). Sapsuckers constantly add new holes to sap wells, and by the end of the season, these wells become impressive feeding sites with hundreds of holes in one area of the tree trunk (Eberhardt 1994). Their heavy use of phloem sap during the breeding season makes Yellow-bellied Sapsuckers ideal organisms for the study of feeding-site choice and sap-extraction techniques.

Phloem sap appears to be an extremely important resource for Yellow-bellied Sapsuckers during the breeding cycle. Nestling sapsuckers remain in the nest cavity for 25 to 29 days after hatching (Winkler et al. 1995). During this entire time, parents use the sap to feed their nestlings by dipping each bolus of insects in the sap before carrying it to the nest (Kilham 1962, 1977). Young that have left the nest cavity also use these major sap wells (Kilham 1962), and the availability of good sap wells may be an important factor during the time that juvenile sapsuckers leave the care of their parents. In short, a high-quality source of sap may be critical to good breeding success during both the nesting and fledgling stages of sapsuckers.

Because Yellow-bellied Sapsuckers feed their nestlings a mixture of insects and sap, they make many trips between sap trees and the nest during the breeding season. Optimal foraging theory suggests that animals should minimize traveling distance to conserve energy (Stephens and Krebs 1986). Thus, my travel-distance hypothesis predicts that sapsuckers will choose trees for sap extraction that are as close to the nest as possible to minimize the energy needed to provision nestlings. Because cavities can be constructed in only a few trees (Shigo and Kilham 1968, Kilham 1977), and the availability of nest sites often is limited for woodpeckers (Welsh and Capen 1992), the distance between the nest tree and sap trees is likely to be more heavily influenced by the choice of sap trees than by the choice of nest trees.

A tree's microsite also can influence the quantity and quality of phloem sap. Microhabitat factors such as water and light availability have an effect on plant sap (Nichols-Orians 1991) and influence how much water is available for sap transport (Hall and Milburn 1973) and how much photosynthate can be transported for storage in the roots (Dale and Sutcliffe 1986). My microsite hypothesis for tree selection predicts that the trees that sapsuckers select for sap extraction will grow in similar microsites with common properties, such as moist soils, high light intensity, and low tree density. Variation among individual trees independent of microsite also can lead to differences in sap quantity, quality, or in how easily sap can be extracted (Gabriel 1982). Sapsuckers may prefer specific trees not because of their lo-

cation, but because of individual variation in sap quality. Such a pattern of tree preference could result from selection for high-quality sap, such as high amino acid or sugar content (White 1984), or an avoidance of sap that may be protected by secondary chemicals in certain trees (Snyder 1992).

Botanists have long noted the phenomenon of sap accumulation in tissue above a girdle or major wound in the woody stems of plants (Salisbury and Ross 1992). Kilham (1964) found that sapsuckers chose trees with rings of old sap holes or other wounds for creation of a new sap well. Sapsuckers also may take advantage of the girdling phenomenon by patterning their current extraction holes to form an ever-widening girdle during the summer. In this way, the birds might cultivate their sap resource over the season. As they make new sap incisions above old ones, the sapsuckers would tap into fresh tissue that has more sap than is contained in tissue from undisturbed boles because the phloem sap is blocked by the girdle from continuing down the trunk. Tate (1973) noted that Yellow-bellied Sapsuckers make new holes directly above old ones into fresh tissue, but no test of increased sap flow as a result of these holes has been made.

I studied the characteristics of sap-well trees of Yellow-bellied Sapsuckers. Detailed observations were made of how the birds make their holes, how long holes flow with sap, and the pattern of holes as they accumulate in a tree's bole. In addition, I experimentally tested the value of making holes in large clusters on trees by testing Kilham's hypothesis that sapsuckers girdle the sap trees with their workings and may obtain more sap as a result.

STUDY AREA AND METHODS

All observations and experiments were made at the University of Michigan's Biological Station in Cheboygan County. The habitat consisted of a mixed hardwood and pine forest that had grown up after major logging operations in the early 1900s. Sapsucker activity was patchily distributed and concentrated in areas of deciduous forest on wetter microsites. I identified all major sap wells used for sap extraction in four main areas of activity during the 1992 and 1993 breeding seasons. Major sap wells were defined as clusters of 100 or more holes on the boles or large branches of living trees and were located by visual survey of the forest and by observing the activity of foraging sapsuckers. For each sap well,

I noted its location on the tree (main bole or major branch), distance to the nearest node of a live branch, presence of old wounds below holes made in the current year, and height above ground. I measured circumference at breast height (CBH) for all trees and when possible climbed to sap wells and measured the tree's circumference at the well. In addition, I noted whether the tree was growing in a clump or as a single tree. A clump was defined as having two or more boles at breast height that appeared to originate from the same root stock. I located active nest cavities by listening for sounds of excavation in April and May of both years and by observing the behavior of birds on their territories.

I compared the properties of trees used for sap extraction with those that were unused. I defined "used trees" as those with at least one major sap well. Occasionally, more than one sap well was active in a tree at the same time. If several stems in one clump had sap wells, I collected one data point only from the clump, assuring that each data point came from an independent plant. Likewise, "unused potential trees" (hereafter "unused trees") were defined as those of the same species as used trees but without major sap wells in them. Data from unused trees were employed as control comparisons with data from used trees and were selected in two different ways (see below). Care was taken in selecting unused trees to assure that they were not connected to trees with sap wells.

Choice of individual trees.—To test the hypothesis that sapsuckers used particular trees because they were close to the nest cavity, I observed whether the trees used for sap extraction were as close as possible to the nest tree. Locations of unused trees were compared with those of used trees with active sap wells. The closest unused tree was identified as the closest one to the nest cavity that was of the same species and of equal or greater CBH as each used tree.

To test the hypothesis that used trees were chosen for their particular microhabitat location, unused trees (controls) were identified as the closest unused neighbor to the used tree of the same species of equal or greater CBH and of equal or lesser distance to the nest cavity. I compared the microhabitat of these pairs by measuring soil moisture and tree density. Soil moisture was measured from a sample of surface soil immediately under the leaf litter 1 m from each tree. Samples for each pair of used/unused trees were taken at the same time. Wet mass was compared with dry mass to calculate percent moisture of each sample. Tree density was calculated by counting all live tree trunks ≥ 5 cm DBH within a 5-m radius of the focal tree.

I used the same pairs of used and unused neighbor trees as above to test for properties of individual trees used for sap extraction. Individual trees were characterized by five variables: health, canopy size, cambial electrical resistance, bark moisture, and bark

thickness. I developed a tree-health index where 1 = most branches dead and only a few living leaves, 2 = more than half of branches dead and all leaves reduced in size or yellowish, 3 = up to half of branches dead and at least some full-sized leaves on tree, 4 = less than one-quarter of branches dead and some leaves reduced, and 5 = completely healthy with no dead branches and all full-sized leaves. Canopy size was estimated with a spherical densiometer. Two estimates were taken on opposite sides of the focal tree's base and then averaged. The densiometer was held against and perpendicular to the bole of the tree at breast height so that exactly half of the concave mirror was filled with the reflection of the tree's bole. The densiometer's mirror was marked with 24 square quadrats, and canopy size was estimated as the number of empty quarter quadrats on the remaining half of the densiometer's mirror that reflected the crown of the tree. Values ranged from zero (completely full canopy) to 48 (no branches or leaves on that side of the tree). Cambial electrical resistance was determined with a model 22-171A Micronta digital multimeter in a manner similar to that used by Shigo and Shigo (1974). Stainless steel electrodes 2 mm apart were inserted into the bark and the minimum electrical resistance (ER) of a pulsed electrical current was recorded for three locations at breast height on the trunk of each focal tree. Cambial ER was used by Mackowski (1988) as a measure of tree vigor in his study of yellow-bellied gliders. Lower values of ER would be expected in trees with more phloem sap or sap with a higher solute content. Two plugs of bark that included all tissue between the outer surface and the sapwood were collected with a 1-cm grommet punch at breast height from each focal tree. Plugs of bark were weighed, dried, and re-weighed for a measure of bark moisture content. Bark thickness was measured as the distance between the outer surface of the bark plugs and the sapwood.

To test whether the use of specific trees could help explain how sapsuckers obtain free-flowing sap from their incisions, I attempted to extract sap from both used and unused trees. I made a variety of incisions, including cutting through the bark to the sapwood with a steel knife, drilling 5-, 6-, and 9-mm holes through the bark with sharp steel bits, chiseling square holes with 6- and 13-mm steel straight-edged chisels, and punching holes through the bark with a grommet punch (as described above). Incisions were made in a variety of locations on experimental trees, including breast height, the center of sap wells, 1 to 2 mm above active sap holes, and approximately 10 cm above sap wells.

Clustering of sap holes.—In four major sap wells, I followed the accumulation of new holes made by sapsuckers through time and recorded number and location of wet holes. A wet hole was defined as one from which sap was flowing. Dry holes may or may not have flowed with sap. I marked individual sap

holes with waterproof ink and periodically returned to them to measure their length and width and to note sap flow and the location of adjacent holes. By returning on subsequent days, I determined how the birds developed their holes and the length of time that each hole exuded sap. I compared data from individual sap wells using ANOVA.

To test the hypothesis that sapsuckers increase the potential to harvest sap by girdling trees with repeated wounding, I set up an experiment to exclude the birds from some of their sap wells. At the beginning of the breeding season, I identified 17 pairs of sap wells with at least 50 old hole scars that had the potential to be used for sap extraction in the current breeding attempt, but were not yet a focus of the sap harvest. Each territory can have as many as 21 old sap wells in living trees, some of which are preferentially attacked as a bird's main sap well for the season (Eberhardt 1994). I matched pairs of old sap wells by size, tree species, territory, and microsite. Then, for one randomly chosen member of each pair, I covered all of the old holes and a zone of approximately 10 cm above these holes with tar paper and duct tape. This prevented the birds from making new holes in or above the covered wells. Covers were left in place during the most active part of the breeding season and removed after 43 to 58 days. At the end of this period, all old and new holes were counted in each well. Because of the self-sealing properties of trees, I was unable to collect phloem sap from trees by incisions into the phloem stream; therefore, I could not compare flow rates between treatments. As a solution to this problem, I measured the percent moisture in plugs of bark and phloem tissue from the experimental and control trees using a grommet punch as described above. Two plug replicates were collected from within 1 cm of the top holes of each sap well. Bird use of the uncovered wells was variable during the season. Because I was testing the effect of repeated wounding, I analyzed only those experimental pairs that had more new holes in uncovered wells than in covered wells at the end of the experiment.

Two types of controls were used in the cover experiment. One controlled for the effect of tar paper coverings on bark moisture. Bark plugs were collected from the bottom of each sap well in an area that was covered by tar paper on the trees in the covered treatment and not covered in the control wells. Bark plugs were collected in the same manner as described above. This allowed me to compare bark moisture between areas of tree trunks covered with tar paper and those not covered without the possible influence of a difference in the number of wounds below each sample location on the trunk. A second control compared bark moisture at breast height on each tree to confirm that no inherent differences occurred in individual trees before attack by the birds.

In addition to the experiment with natural wells, I

constructed artificial sap wells in 10 trees by repeatedly wounding the trees throughout the breeding season. These trees were of the same species and size as those used by sapsuckers for sap extraction, and all of them were located on active sapsucker territories. During a 44-day period, I drilled a combination of 5-, 6-, and 9-mm holes in a pattern of vertical lines similar to that made by sapsuckers. I added 10 to 15 new holes approximately every four days to each well during this period. At the end of the experiment, I removed bark and phloem tissue samples with the 1-cm grommet punch to test for changes in moisture levels resulting from repeated wounding. Plug samples were taken within 1 cm of the top holes and 20 cm above the artificial well on the bole of each tree. Moisture levels between the plugs at the top of the wells and ones from 20 cm above the wells were compared. Wilcoxon signed-rank tests (Hollander and Wolfe 1973) were used for comparisons of all paired data described above.

RESULTS

Of 36 active sap-well trees that I observed in 1992 and 1993, 17 were in birch (*Betula papyrifera*), 8 in red maple (*Acer rubrum*), 6 in juneberry (*Amelanchier* sp.) and 5 in bigtooth aspen (*Populus grandidentata*). Two of the sap wells were constructed on large branches, and the rest were located on the main bole of trees. Sapsuckers attacked trees that were located in clumps that included other used trees more often than they attacked single trees or trees located in otherwise unused clumps. Of 19 independent woody stems originating from different root stock and containing sap wells, 13 were in clumps with other used trees. Sap wells were located at an average height of $7.1 \pm \text{SD of } 3.5 \text{ m}$ ($n = 19$) on trees, and 18 out of 19 were within 1 m of the node of a live branch. Sap wells observed in 1993 had an average circumference at the bottom of the sap well of $39.1 \pm 13.3 \text{ cm}$ ($n = 20$) and an average CBH of $64.0 \pm 39.9 \text{ cm}$ ($n = 20$).

Old scars left by wounds from previous years were sometimes difficult to see, especially in used trees that could not be climbed, forcing observation from the ground. Of 20 individual sap wells observed in 1993, at least 17 were constructed immediately above scars left by sapsucker holes from previous years. Only one of the remaining three sap wells was unmistakably in a fresh, unscarred tree; the other two were too high to determine the presence of scars left by old wounds.

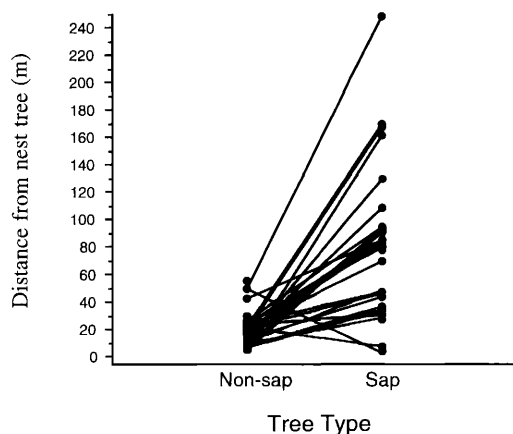


FIG. 1. Paired comparisons between the distance from nest trees to trees used for sap extraction and the distance from nest trees to the closest unused trees of the same size and species as the tree used for sap extraction.

Choice of individual trees.—Yellow-bellied Sapsuckers chose trees for sap extraction that were farther from their nest than unused trees of the same species and size ($T^+ = 14$, $n = 24$, $P = 0.0001$). Pairs of sapsuckers traveled an average of 64.9 m farther than needed to find a tree of the appropriate size and species to reach a tree used for sap extraction (Fig. 1).

Measurements of microhabitat, including soil moisture and tree density, did not differ between trees used for sap extraction and their nearest unused neighbor of the same species and equal or greater CBH (Table 1). In addition, measurements of individual variation such as crown size, bark thickness, and bark moisture also did not differ between used and unused trees. However sap trees had a lower health index than unused trees ($T^+ = 5$, $n = 14$, $P = 0.003$).

I obtained sap only when my incisions were made within 0.5 cm above active sapsucker holes, and then only after sapsuckers had access to my holes for a few hours. Incisions made 10 cm or more above or within the sap wells of these same trees did not yield sap. In no other situation did sustained sap flow occur at my incisions in either used or unused trees.

Clustering of sap holes.—Daily observations of four undisturbed sap wells revealed several interesting details of the sapsuckers' wounding techniques. Sapsuckers added new holes to existing wells immediately above old holes with-

TABLE 1. Comparisons between trees used for sap extraction and neighboring unused trees. Values are $\bar{x} \pm$ SD; *P*-values are from Wilcoxon signed-rank tests.

Variable	<i>n</i>	Used tree	Unused tree	<i>P</i>
Microhabitat				
Soil moisture (%)	17	12.6 \pm 5.25	14.7 \pm 6.29	0.463
Tree density (no. per 20 m ²)	16	7.8 \pm 3.2	7.0 \pm 3.8	0.478
Individual differences				
Crown size (no. open quarters)	16	4.2 \pm 3.2	5.4 \pm 4.1	0.313
Bark thickness (mm)	18	6.5 \pm 2.5	6.5 \pm 4.1	0.763
Bark moisture (%)	19	37.1 \pm 6.42	36.6 \pm 4.73	0.601
Health index	19	3.2 \pm 1.1	4.5 \pm 0.9	0.003
Cambial ER (k-ohms)	18	46.7 \pm 27.5	92.2 \pm 181.8	0.085

in 0.5 cm of the top of a previous hole. New holes were started as small horizontal ovals through the bark and phloem tissue to the surface of the xylem and then were enlarged by successive cuts into fresh tissue above the wound (Fig. 2). Holes were enlarged for several

days in a row, and sap could be collected from each individual hole for an average of 3.1 ± 1.8 days ($n = 51$ holes) before sap flow ceased. The four sap wells differed in the number of new holes added by the birds each day ($F = 39.52$, $df = 3$ and 36 , $P = 0.0001$; Table 2). As the sea-

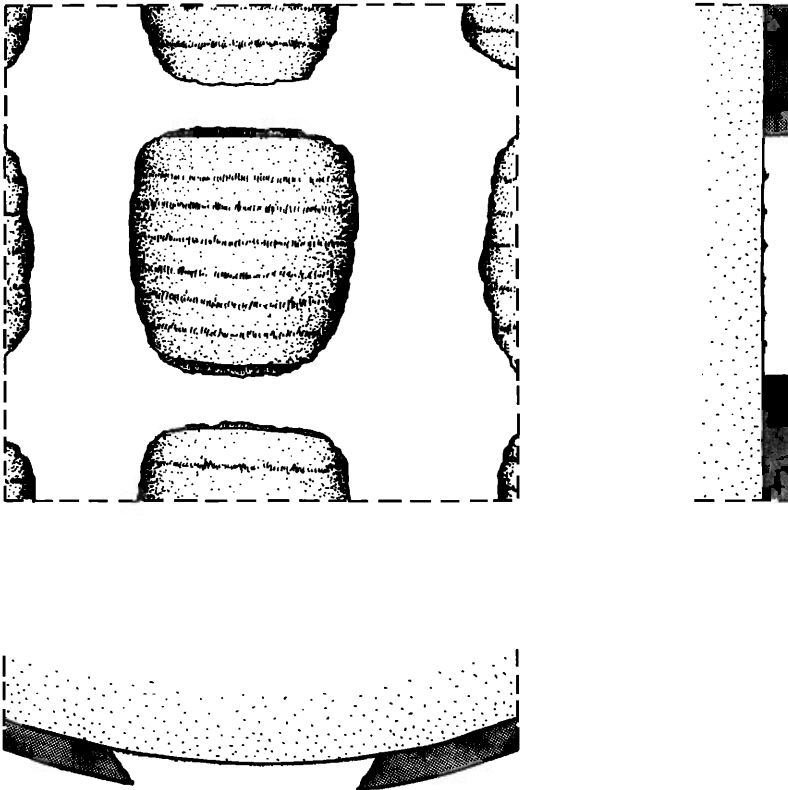


FIG. 2. Representations of a typical completed sap hole cut in the bark for phloem sap extraction. Frontal view (upper left) shows faint lines left from successive enlargements. A longitudinal section (upper right) reveals that the top and bottom edges are cut perpendicular to the surface of the xylem tissue. A cross section (lower left) shows that the sides are made at an acute angle to the back surface of the hole. Gray areas on longitudinal and cross sections denote the bark of the tree.

TABLE 2. Number of new holes added per day ($\bar{x} \pm$ SD) in each of four sap wells.

Sap well	No. of new holes per day	No. of days
Aspen 1	5.7 \pm 2.8	17
Aspen 2	2.0 \pm 1.0	7
Juneberry	20.0 \pm 5.9	5
Birch	5.9 \pm 1.9	8

son progressed, each sap well increased in size by expanding vertical lines of holes up the tree's bole, with only the top-most holes actually producing sap at any given time (Fig. 3).

In the sap-well cover experiment, three of the experimental pairs were eliminated from analysis because the wells that had been left uncovered did not have more new holes than those that were covered. Of the remaining experimental pairs, moisture levels in bark and phloem tissue increased an average of $7.34 \pm 2.52\%$ in sap wells that had been repeatedly wounded by sapsuckers relative to ones that were excluded from the birds' use ($T^+ = 16, n = 14, P = 0.024$; Fig. 4). This increase did not result from the tar paper covering ($T^+ = 54, n = 16, P =$

0.469) or from intrinsic properties of individual trees that were included in the experimental treatment ($T^+ = 43, n = 13, P = 0.861$). In the artificial sap wells that I made over a 44-day period, bark moisture above artificial holes and bark moisture away from the artificial wells did not differ ($T^+ = 26, n = 10, P = 0.878$).

DISCUSSION

Yellow-bellied Sapsuckers did not prefer to extract sap from trees close to their nest trees even though trees of the appropriate species and size often were available nearby. Thus, I can reject the hypothesis that sap trees were selected to minimize travel distance during nesting. Sapsuckers traveled great distances to reach individual trees that were appropriate for sap extraction.

Sapsuckers did not appear to seek out specific microsites for sap trees. The microhabitat of the sap tree can be one factor that influences the quality of phloem sap (Dale and Sutcliffe 1986). However, I found no indication that sapsuckers preferred trees in wetter sites or trees that grew in lower densities that might indicate

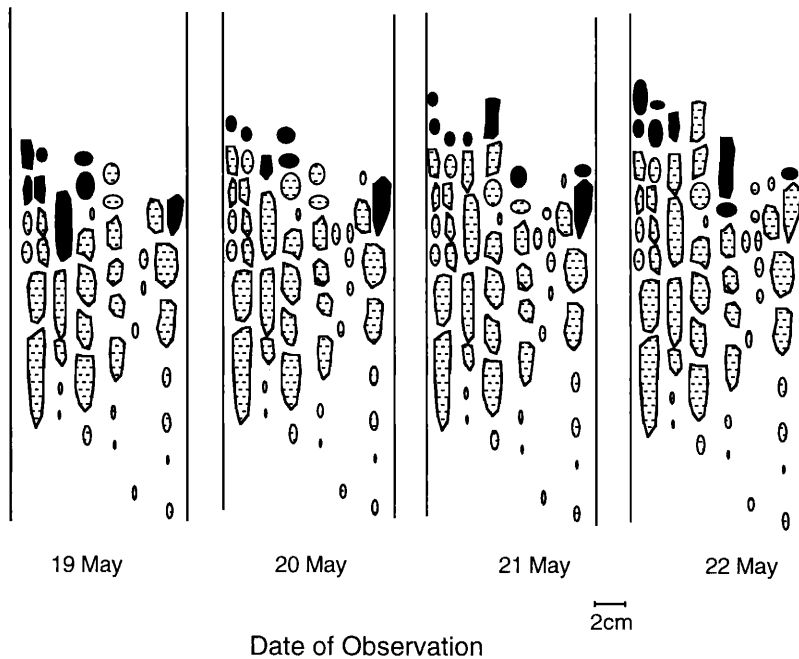


FIG. 3. Changes in a sap well over four days in May 1993. Darkened holes designate those with sap flow, and stippled holes are dry and no longer produce sap. Note how new holes are added above older holes.

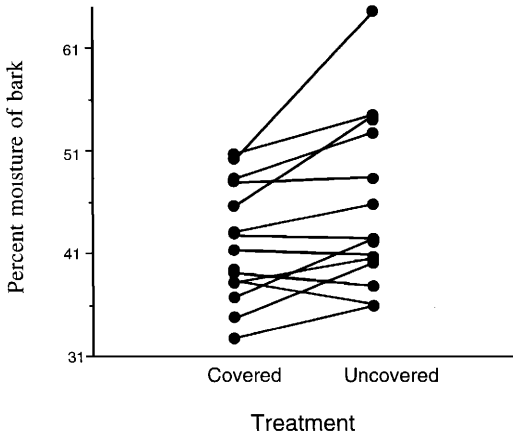


FIG. 4. Paired comparisons of moisture content of bark and phloem tissue in trees that sapsuckers were prevented from using (covered) and those that sapsuckers continuously wounded during the breeding season (uncovered).

that they received more light or experienced less competition. Therefore, I suggest that sapsuckers prefer trees for their individual qualities and not for their microhabitat or location relative to the nest cavity.

I found a striking difference between the health index of trees that sapsuckers used for sap extraction and neighboring unused trees. Trees in poor health could be either a cause of sapsucker preference or an effect of their attack. Trees that are in poor health or in the beginning stage of senescence are likely to have higher levels of amino acids in their phloem sap (see White 1984). Because nitrogen often is a limiting nutrient for phloem-feeding animals (Fitter and Hay 1987), sapsuckers may prefer to eat sap from dying trees because this sap offers a more balanced nutrition than sap from healthy trees. In addition, repeated wounding such as that done by sapsuckers could increase stress and induce a release of proteins into the phloem sap. In an analogous technique, a bruising method called "cinching" has been used by orchard growers to stimulate fruit production (Owen and Weigert 1982, White 1984). Thus, sapsuckers may choose dying or stressed trees and repeatedly wound them in a way that increases protein availability and sap flow. This repeated wounding may itself have an effect on tree health. Sapsuckers may choose healthy trees for attack, but as they slowly girdle the tree with their wounds, the tree dies. Such a

scenario was suggested by Tate (1973), who found that an average of 3.75 sap trees died per year on a sapsucker territory that he followed for four years. Thus, although it is clear that the trees that sapsuckers attack are less healthy than surrounding trees, without more information, firm conclusions cannot be drawn about whether sapsucker use is a cause or an effect of this phenomenon.

The fact that sapsuckers appeared to preferentially attack multiple stems in clumps of trees rather than single isolated trees suggests either that all stems a clump are equally attractive for sap production, or that the available trees of the correct species are a limited resource and are located in clumps. Tate (1973) found that on one sapsucker territory, the birds attacked only 2 of the 27 birches available. Other observations also suggest that the availability of the appropriate species for sap collection is not limiting (Eberhardt 1994). Thus, some characteristic of the stems of particular clumps may be responsible for attracting sapsuckers. Several factors could explain this preference, including the history of past wounding (see below), genetic differences, or variation in pathogen attack (see Linhart 1989). However, thus far I cannot clearly separate the effects of these possibilities on tree preferences of sapsuckers.

I found no significant differences between used and unused trees in cambial electrical resistance, bark moisture, crown size, or bark thickness. However, an extremely large variance in cambial electrical resistance measurements may not have allowed detection of significant differences with my sample size. On average, cambial electrical resistance was much lower in trees used for sap extraction (Table 1). This may indicate that these trees had more sap, or a higher solute content in their sap, which made them attractive for sap extraction. Thus, although sap quality may be influenced by the underlying genetics or disease state of the trees, without more information I cannot determine exactly what the birds preferred in the trees that they used for sap extraction. Although I cannot be sure that I constructed my holes in the same mechanical way that sapsucker use, my failure to induce sap flow from incisions in both used and unused trees probably indicates that sapsuckers do not prefer specific trees solely for their poor phloem-sealing properties. Other possible differences be-

tween used and unused trees that remain to be explored include content of plant secondary compounds, solute content of sap, and production of exudates to seal wounds.

At least 85% of all major sap wells observed during this study were constructed above scars left in the phloem as a result of old wounds. As predicted by the wounded-tree hypothesis, sapsucker preference for individual trees may result from historic use of particular trees in the area. If, during the breeding season, a few holes are made to wound the unused trees surrounding the current active sap well, then in the following year, major sap wells could be constructed above these wounds. Such a scenario would explain why sap wells tend to be located in clumps of trees, because after a few years of such girdling, old and new used trees would be centered around areas of high activity. Indeed, this is exactly what Tate (1973) suggested to explain the formation of "sap orchards," which are areas that are so extensively used by sapsuckers they eventually must be abandoned.

In addition to taking advantage of the effects of wounds and scars from previous years, Yellow-bellied Sapsuckers also may induce increased sap flow by the pattern of wounding that they use during one breeding season. Their method of hole construction involves continued cuts into fresh phloem cells each time the hole is enlarged over its lifetime of several days. New holes are started above previous holes, which eventually creates long vertical lines of holes with blocked phloem tissue. This type of wounding appears to act as a dam in the phloem sap stream that allows the build-up of sap in tissues above the dam. Indeed, the moisture content in bark of attacked trees increased above holes made for sap extraction during a period of 6 to 8 weeks. It appears that sapsuckers may increase their chances of successful sap extraction with a repeated wounding technique. However, my attempt to create artificial sap wells failed to induce sap flow or increase bark moisture. My technique of drilling holes may not have mimicked the sapsuckers' hole constructions closely enough to induce sap flow. Alternatively, my drillings may have been adequate mimics of true sap holes, but the sapsuckers may employ additional (as yet unknown) techniques to induce sap flow.

I found that Yellow-bellied Sapsuckers usu-

ally located sap wells below branch nodes on the main tree bole of a selected tree. Such placement would take maximum advantage of photosynthate coming from the leaves on that main branch as well as from the rest of the tree's crown. Sapsuckers rarely made sap wells below 3 to 4 m from the ground, which may reflect better locations for sap extraction higher in a tree (i.e. closer to sources of phloem sap). However, predation avoidance is an alternative explanation for these feeding patterns because feeding under branches would shield sapsuckers from aerial predators, and staying away from the ground would protect against attack from below. As with other aspects of sap feeding in these intriguing birds, more research is needed on how predation influences sap-extraction behavior.

By testing alternative hypotheses for sap-tree preference and wounding techniques, I found evidence that sapsuckers choose trees because of the tree's individual properties, rather than their location, and that sapsuckers appear to cultivate their sap resource by repeated wounding in the form of clusters of sap holes on tree boles. However, how sapsuckers actually induce sap to flow from these holes remains unknown. The only cases where sap flowed from my artificial incisions were situations where sapsuckers used my hole first for a few hours. Perhaps sapsuckers process their holes in ways that induce sap flow, such as adding saliva as an anticoagulant (Eberhardt 1994), but the exact mechanism of sap extraction remains a mystery. What is clear is that sapsuckers are somewhat unique in their ability to mine sap, and many species steal sap and even rely on sapsucker sap as a food resource (Southwick and Southwick 1980, Daily et al. 1993). Because trees may die as a result of sapsucker attack, and many animals may need sap for food, how sapsuckers choose their trees and extract sap from them has far-reaching implications for the whole forest community.

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