REPRODUCTIVE BEHAVIOR OF YELLOW-BELLIED SAPSUCKERS
I. PREFERENCE FOR NESTING IN *FOMES*-INFECTED ASPENS AND NEST HOLE INTERRELATIONS WITH FLYING SQUIRRELS, RACCOONS, AND OTHER ANIMALS

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A concept presented below is that woodpeckers have search images of optimal nest trees and in this regard Yellow-bellied Sapsuckers (*Sphyrapicus varius*) are attracted to mature aspens (*Populus tremuloides*) bearing conks of the false tinder (*Fomes igniarius* var. *populinus*) (Shigo and Kilham, 1968). The fungus renders these trees particularly favorable in several ways: first in inducing extensive decay of the heartwood (Fig. 1) and second in sparing the sapwood which remains as a tough outer living shell protecting the nest cavity. As described below, sapsuckers may re-nest in a suitable aspen over many years. Selection pressures which may operate in formation of search images form the basis of a final discussion. Those emphasized in the following accounts being predation by raccoons (*Procyon lotor*), close association with tree squirrels and, to some degree, interspecific competition with Hairy Woodpeckers (*Dendrocopos villosus*).

This report is based on 50 nestings, of which 29 were in aspens, noted between 1958 and 1970 in Tamworth and in Lyme, New Hampshire. Reports giving background to these studies on sapsuckers are one on breeding behavior (Kilham, 1962*a*) and another on feeding behavior (Kilham, 1964).

Other accounts of nesting sapsuckers are given by Bent (1939) and by Lawrence (1967). Both authors mention aspens as nest trees but do not discuss the role played by *F. igniarius*. Philipp and Bowditch (1917), however, noted of *S. varius* in New Brunswick that "The favorite (nest) situation was the dead heart of a live poplar."

NESTINGS OF SAPSUCKERS IN FOMES-INFECTED ASPENS

The tinder fungus infects a wide variety of trees and sapsuckers may nest in butternuts (*Juglans cinerea*) and in beech (*Fagus grandifolia*) as well as in aspens infected with them. A number of attributes, however, such as the type of decay, the straightness of the bole, and usual diameter when mature (20 to 25 cm) make aspens particularly favorable as nest sites. The nature of the decay has already been described in a note by Shigo and Kilham (1968). As shown in Figure 1 the area of softening and discoloration may extend for a distance up and down the bole from the vicinity of a conk

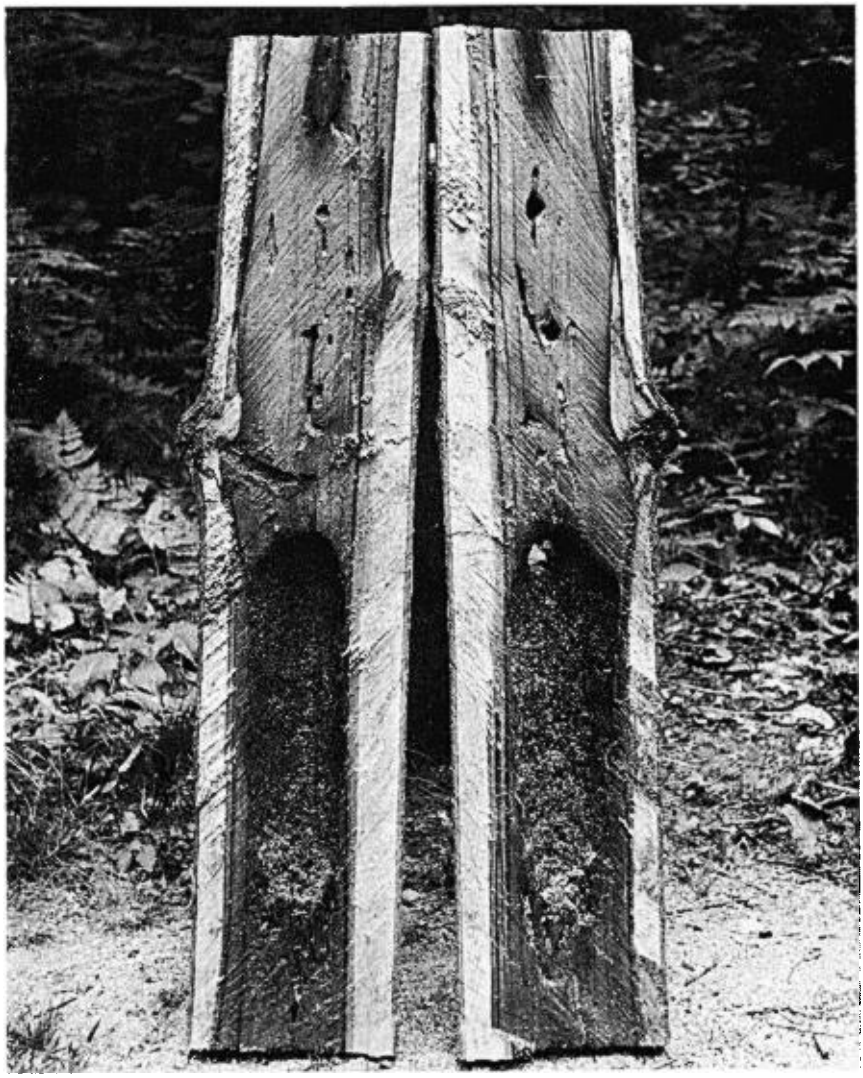

FIG. 1. Longitudinal cross section of an aspen (age 75 years and 22 cm dbh) showing extensive heart rot as well as conks of *F. igniarius*. Tunnels above and below, as well as frass in bottom of the nest cavity of a sapsucker are due to carpenter ants.

or sporophore leaving the sapwood unaffected, a nest entrance (Fig. 2) made through 3 cm of such wood being more or less impregnable to likely predators.

In the following accounts I have designated sapsuckers occupying the

FIG. 2. Longitudinal and front view of the nest of a sapsucker in a mature aspen (age 65 years and 20 cm dbh), in which area of heart rot due to *F. igniarius* is more limited than in Figure 1.

same territory in successive years by the same letter even though individuals making up the pair might change. Thus, Pair A 1963, for example, was a definite pair, just as Pair A 1969 was another.

Territory A.—I located the first nest hole in Aspen A, which had many

TABLE 1

OBSERVATIONS MADE OVER A 6-YEAR PERIOD OF A PAIR OF SAPSUCKERS IN TERRITORIES A AND B, SHOWING PERSISTENCE OF ATTRACTION TO ASPENS INFECTED WITH *FOMES IGNIARIUS* AS NEST TREES

Year	Height of Nest Hole	Date of Nest-leaving	Special Events
		Territory A (Nested in single aspen 5× in 6 years)	
1963	7m	6 July	Hole chewed by raccoon 1 July (no harm).
1964	6m	29 June	1963 nest hole occupied by flying squirrel.
1965	10m	Trial excavation only. No nest	——
1966	8m	23 July	——
1967	12m	14 July	——
1968	13m	28 June	——
		Territory B (Nested in successive *Fomes*-infected trees)	
1963	6m	4 July	Nest in butternut infected with *F. igniarius.*
1964	7m	5 July	Dying *Fomes* aspen. Last year used.
1965	11m	Nest failed.	*Fomes* aspen too narrow for normal nest cavity.
1966	nest not found	Juveniles seen in July.	20 April—trial excavation in "healthy" aspen.
1967	5m	5 July	Dying aspen.
1968	8m	20 June	Same dead aspen used successfully 1968 and 1969.

conks over a 10 cm extent of the bole in 1963. From the time the young sapsuckers hatched on 12 June until they left the nest on 6 July (see Table 1) they made a persistent and increasing volume of harsh vocalizations. Such vocalizations may have survival value among sapsuckers in keeping the parent birds steadily on the job of collecting food. One may wonder, however, whether the noise might not also attract predators, for on the morning of 1 July I found a rosette of tooth marks around the bark of the nest entrance. Similar tooth marks, which I have found on other nest aspens

along with claw marks and bits of fur have indicated that such attacks are probably all made by raccoons. The attack made on the nest of Pair A had no apparent effect as the young left successfully 5 days later.

A second nesting of sapsuckers in Aspen A was equally successful in 1964. In 1965 sapsuckers started an excavation in late April. They had abandoned it by 2 May and it is conceivable that in such cases the fungus decay may not have advanced sufficiently within the heartwood to furnish another site as one can see for example in Figure 2. Such decay takes time. After a year away the sapsuckers returned to nest successfully in the aspen in 1966, 1967, and 1968 (Table 1), but failed to return in 1969 when the aspen was still alive. With 5 nest holes in addition to an equal number of trial excavations it resembled a much used tenement house with possibly no space left for an additional cavity.

I judged nesting success among sapsuckers from several lines of evidence. The most satisfactory of these was presence of juveniles on nearby trees on the morning of nest leavings as happened in the 1966, 1967, and 1968 pairs in Aspen A. Juveniles may leave the vicinity of the nest within an hour or less. This makes them difficult to locate and in 1963 and 1964 I considered nestings of the pair successful when full grown young were putting heads out of the entrance one day and were gone the next without signs of the nest having been destroyed.

I was not sure how many individuals had been involved in the various nestings of pairs using Aspen A between 1963 and 1968. In 1967, however, certain peculiarities marked the individuals of the pair as the ones which returned to nest in 1968. The female of both years was a black morph, having a black instead of red crown, and her mate almost invariably used a particular location on the bark of a small hornbeam to discard sawdust and feces after he had cleaned the nest (Kilham, 1962*b*).

Territory B.—The sapsuckers occupying this territory nested in a butternut in 1963 and in an aspen in 1964, both trees bearing prominent conks of *F. igniarius*. The aspen had died by 1965 and was not re-used. I had come to believe by this time that sapsuckers would only nest in aspens that were still alive even if barely so, as was true for the one used by Pair B in 1967. This tree had died by 1968. To my surprise, however, the sapsuckers made fresh excavations and nested successfully in the dead aspen in both 1968 and 1969 (Table 1).

1965 was a difficult year for Pair B and exemplifies the efforts sapsuckers can made to nest in *Fomes*-infected aspens. On 24 April, for example, I found the female working a small funnel-shaped excavation in the smooth bark of a seemingly healthy aspen. This seemed unusual for I could see no conks. Closer inspection, however, revealed three small ones where the

female was working. The smoothness of the bark below made it difficult for her to cling and she slipped several times, each time fluttering back to regain her position. A few days later I found that she had roughened the bark over a 6 by 10 cm space below the hole and on 26 April she bent down to roughen it a bit more. Although now able to grasp the bark securely she made little headway with her excavating in this relatively sound tree with little inner decay.

The sapsuckers of Pair B were working on a second *Fomes*-infected aspen by early May. The tree had many mature conks but was unusual in having a diameter of only 12 cm and a long, spindly, crooked bole obviously unsuitable for nesting. The sapsuckers, however, continued to excavate in relays and on 7 May they were able to enter their excavation completely. For the next 3 weeks I was never sure just what they were doing. They visited their crooked aspen repeatedly, performed a variety of courtship displays, and yet gave no signs of nesting. They finally abandoned the tree in early June and I was puzzled to know the reason for failure after so much effort. I therefore cut the aspen down and found that the cavity within had a surprising shape. With a diameter of 8.6 cm and a length of 51.4 cm it was narrower as well as twice as deep as a usual nest and resembled a long, narrow mailing tube. The excessive depth was probably due to the marked slant of the bole which allowed light rays to penetrate farther down than usual.

ATTACKS BY RACCOONS

I had to come to feel by 1967 that sapsuckers nesting in *Fomes*-infected aspens had excellent chances of nesting success, as only one of 10 nests in such trees had failed. In 1967, however, I encountered three nests in *Fomes*-infected aspens that were destroyed by raccoons. Details of events at two of these followed most closely were as follows:

Pair W.—Female W had already lost her mate when I first found her nest in a live *Fomes*-infected aspen on 24 June. I was surprised to find her still caring for her nestlings as a lone parent a week later. This was the last time she did so. On the following day, 2 July, there were fresh raccoon gnawings around the entrance in addition to an old set which had been there when I found the nest originally. I now searched the ground and found two piles of feathers. One of these apparently belonged to the male that had been killed before I found the nest. These were old and matted, as though exposed to the weather for a week or more, and contained 31 wing and eight tail feathers. A second pile a few meters away from the first had 26 wing and seven tail feathers. These were fresh and obviously those of the female. It is difficult to know why the raccoon had succeeded so well. The nest entrance was located 10 m above the ground and I wondered whether the nest cavity may not have been too shallow, the sapsuckers having been limited in their excavating by the insufficient extent of fungus decay. Thus, the

raccoon must have reached through the entrance and caught the sapsuckers with a paw, for it had not been able to enlarge the hole by chewing around it.

Pair C, 1967.—A raccoon had already attacked nest C, located only 2 m up, when I found it on 5 June. The ring of tooth marks became more extensive following a second attack on 7 June, but the sapsuckers continued feeding their young in usual fashion until 20 days later. At this time the raccoon made what must have been a prolonged attack. So much bark had been chewed away that I could see the exposed white sapwood of the aspen from a distance and I was not surprised to find that the male had been killed, a pile of his feathers lying below the nest. The raccoon, however, had not destroyed the entrance. I thus imagined that by continually reaching into the nest, while snarling and biting, the raccoon may have finally gotten the over-excited male to come within reach of one of his paws.

The female now fed her nestlings alone for 2 days during which time she attracted a new mate, who, to my surprise, was feeding his adopted young on 29 May. The raccoon made a fourth attack on the following night. The gnawing and bite marks around the entrance were even more extensive than those seen previously. The well-grown nestlings had all been pulled out through the still intact entrance and their feathers lay on the ground. One might ask why the raccoon had been so successful at this nest hole, built as it was in a seemingly ideal aspen which, I found later, had provided ample inner decay for a nest cavity 25 cm in depth. It seemed likely that the closeness of the nest to the ground was what attracted the raccoon. At 2 m it was the lowest nest of all the 50 which I have found and this accessibility may have made the raccoon far more persistent than he would have been had the nest hole been located higher up.

CARPENTER ANTS

A nest which may have been disturbed sufficiently by carpenter ants (*Camponotus pennsylvanicus*) to lead to its abandonment was that of Pair E in 1965. The entrance was 8 m up above swampy ground and the sapsuckers had been feeding their young for a week when, on 12 June, I found that a raccoon had gnawed the entrance. The attack seemed to have had little effect. The living sapwood had withstood the attack and I watched the male feeding its young on the following morning. I was, therefore, puzzled to find the nest deserted a week later. The nestlings had not been old enough to leave in so short a time and, seeking a clue, I cut the aspen down. I then found that carpenter ants had tunnels leading into the nest cavity. There was no proof that the ants had caused the destruction of the nest. They had, however, partially filled it with frass and it is conceivable that their activities, especially at night when the sapsuckers might not be able to see and protect themselves, might have led the sapsuckers to leave.

Figure 1, while of a different tree than that of Nest E, is a longitudinal section of a *Fomes*-infected aspen showing tunnels of carpenter ants above and below a sapsucker nest cavity as well as an accumulation of frass at the bottom of it.

INTERRELATIONS WITH SQUIRRELS

Of the three arboreal squirrels found in New Hampshire, the gray squirrel (*Sciurus carolinensis*), the red squirrel (*Tamiasciurus hudsonicus*), and the flying squirrel (*Glaucomys* sp.),* the last two are somewhat dependent on the excavations of Hairy Woodpeckers and sapsuckers for secure resting as well as nest holes. Sapsuckers nesting in straight aspens within woods appear to be of particular importance to flying squirrels which almost invariably occupy old sapsucker nest holes sooner or later. This leads to close interrelations, especially where the sapsuckers return to nest in the same tree in a following year. As described below sapsuckers appear able to cope with squirrel neighbors without undue excitement.

Pair D, 1965.—In the spring of 1965 I had found a flying squirrel occupying the 1964 nest hole of this pair. The returning sapsuckers excavated a new hole only 30 cm above the one occupied by the squirrel. A low afternoon sun attracted the squirrel to look out on both 5 June, as well as inducing the male sapsucker to stop incubating, at least temporarily, to catch insects close to its nest. The male sapsucker attacked the squirrel by swooping at it six times and followed through by clinging to the outside of its hole and pecking down as the squirrel withdrew. The squirrel seemingly unfazed by the attacks put its head out again after the bird had left.

Pair C, 1969.—The sapsuckers of Pair C nested in one *Fomes*-infected aspen from 1963 through 1970, with the exception of a single year, 1967. I had found flying squirrels occupying their old nest holes over a number of years and on observing that the sapsuckers were behaving in an unusual manner on 13 June, I wondered whether a flying squirrel might be responsible. The nestling sapsuckers in this nest had hatched about 10 days previously. First one parent, then the other, would stay in the nest looking out until relieved by its mate arriving with a bill full of insects caught in the immediate vicinity. After 10 minutes of watching I saw a gray squirrel raise its head in the gnawed entrance of a hole several meters below the nest of the sapsuckers. Either of the parent sapsuckers arriving at the nest would first turn its head to eye the squirrel before feeding the young. Neither bird, however, attacked the squirrel or gave signs of alarm.

On the following noon I found the sapsuckers of Pair C behaving in similar fashion. I then sat down at a distance expecting to see the gray squirrel appear again. To my surprise, however, a red squirrel came down past the sapsucker's hole and squeezed into another old nest hole about 30 cm below the one occupied by the gray squirrel the day before. The red squirrel put its head out, rested 5 minutes and then came out. Passing by the sapsucker's nest a second time it leapt onto branches of other trees and did not return. The sapsuckers changed their behavior immediately by ceasing to guard their nest hole and as is the usual behavior of sapsuckers with advanced nestlings flying away after a few brief seconds of feeding their young to catch more prey.

Pair C, 1967.—Sapsuckers and Hairy Woodpeckers which use nest trees of the same general diameter appear to have differing reactions to flying squirrels. A pair of Hairy

*There are two sympatric species of flying squirrel in central New Hampshire, *G. volans* and *G. sabrinus*. I was, unfortunately, unable to identify them as to species from just seeing a head in a nest hole, for they are difficult to distinguish unless seen at close range.

Woodpeckers in 1965 nested in a typical *Fomes*-infected aspen used by the sapsuckers of Pair C in 1967. Flying squirrels took over the woodpecker's old nest hole later on, enlarging the entrance to such an extent that in July 1966 heads of four squirrels shot out simultaneously when I knocked below. Presence of one or more squirrels in this hole did not deter Pair C from using the aspen in 1967. Their new excavation was only a meter below the one being used by the squirrels. The squirrels remained in residence here until near the end of the sapsucker nesting period. I have wondered in such cases, of which I have observed two, whether the almost incessant, harsh, clambering of nestling sapsuckers made during the day when squirrels would normally be sleeping, might not lead them to move to a cavity in some other tree.

This nesting of the sapsuckers and Hairy Woodpeckers in the same *Fomes*-infected aspen, although in different years, has interest in showing that both species, which have approximately the same body size, have essentially the same requirement in the bole diameter of potential nest trees.

NESTINGS IN TREES OTHER THAN ASPENS

Sapsuckers, like other woodpeckers, will nest in trees and stubs that are far from optimal through necessity and this probably explains why 21 of 50 nestings encountered were not in *Fomes*-infected aspens but in stubs or in dead portions of otherwise living trees such as elms, maples, paper birches, and beeches. These latter nestings were not followed closely, some having been seen but once on remote mountain trails and three having been interrupted to procure young for hand-raising. What appeared common to all, however, was that they were in woods either without aspens or without those rare ones which have the right diameter combined with extensive heart rot due to *F. igniarius*.

Three of the nests found in other than aspens and followed subsequently were destroyed by raccoons. Here the animals, with only dead, rotten wood to chew through, appeared to have had an easy time breaking through the front, side, or rear (see Fig. 3) of a nest cavity, whichever was weakest.

COMPARISONS WITH OTHER SPECIES

The idea of a search image is almost classically illustrated by the Red-cockaded Woodpecker (*Dendrocopos borealis*) which, to draw upon Steirly's (1957) account of this species in eastern Virginia, nests almost exclusively in mature loblolly pines (*Pinus taeda*) affected with heart rot due to *Fomes pini*. There is, of course, the difference that sapsuckers live in a more varied habitat and are *eurytopic*, whereas *D. borealis* is notably a *stenotopic* species. An interesting and recent account of the nesting of *D. borealis* is that of Ligon (1970).

Hairy Woodpeckers are sympatric with sapsuckers in New Hampshire have a search image of an optimal nest tree which overlaps that of sapsuckers to some extent, for the two species are close enough in body size

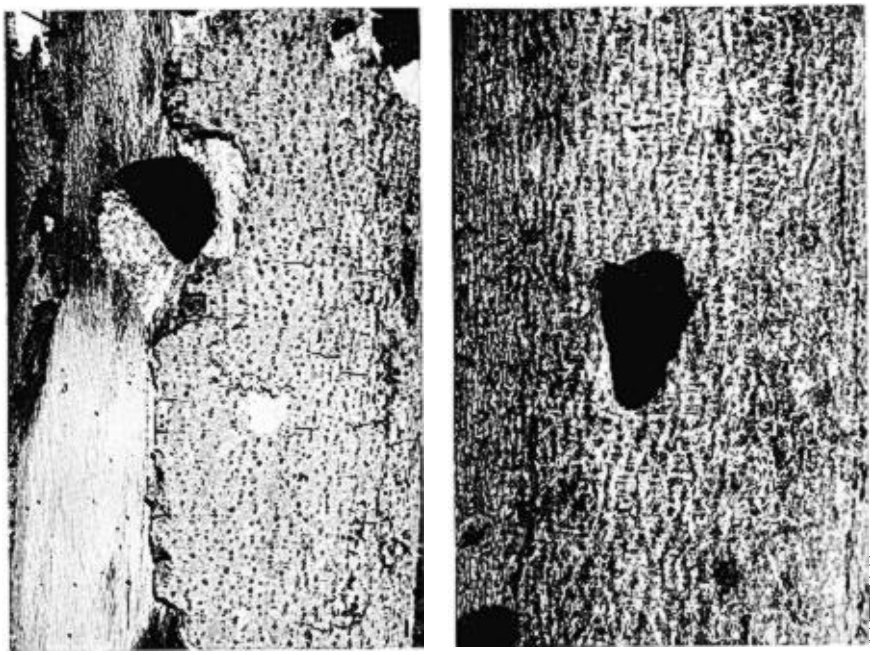

FIG. 3. Front (a) and rear (b) views of the nest of a sapsucker in the bole of a dead beech. Although the entrance (a) was made through 4 cm of solid wood, a raccoon was able to destroy the nest by breaking through the back (b) which was 1 cm or less in thickness.

to require the same outside nest diameters. Neither these nor any other species of eastern woodpecker can excavate a nest cavity in solid wood. The most they can do is excavate an entrance through living sapwood and here even Hairy Woodpeckers, with stronger bills than sapsuckers, are also dependent on heart rot produced nearly always by *F. igniarius* which infects a wide range of tree species in addition to aspens.

Table 2 gives the hypothetical search image of an optimal nest site for Hairy Woodpeckers. It lies in open situations and when the woodpeckers are forced to seek a site in woodlands due to pressure from starlings (*Sturnus vulgaris*) or other reasons, they may come into competition with sapsuckers (Kilham, 1969). An hypothesis as to why they generally do not do so, however, relates to flying squirrels. These animals favor nest cavities high up in straight boles of trees and on three occasions I have found where they had apparently taken over the nest holes of breeding Hairy Woodpeckers (Kilham, 1968). I have never, however, noted flying squirrels displacing nesting sapsuckers in such situations. The strategy of sapsuckers, be it

TABLE 2

SEARCH IMAGES OF OPTIMAL NEST TREES OF YELLOW-BELLIED SAPSUCKER AND HAIRY WOODPECKER IN NEW HAMPSHIRE

Woodpecker Species	Search image of optimal nest site	Selection Pressures		
		Predator	Nest-hole Competitors	
		Procyon lotor	*Sturnus vulgaris*	*Glaucomys* Sp.
D. villosus	On underside of curved limbs of trees growing in moderately open situations.	Highly successful in destroying nests located in less than optimal situations.	Dispossesses *D. villosus* from holes in straight tree trunks, but avoids nest holes on the under side of limbs and near foliage.	Frequently dispossesses woodpeckers nesting within woods, especially where nests are high in boles of straight trees.
S. varius	Mature, straight aspen in woods bearing conks of *F. igniarius*.		Not attracted to sites within woods. Hence not a competitor.	Not competitors for new sapsuckers nest holes due to prior occupation of old ones.

innate or coincidental, is that by re-nesting in aspens they provide flying squirrels with what are ideal nest cavities. The squirrels, being well established when the sapsuckers return in a following year, have no incentive to face attacks of these birds to move from where they are already well established to new excavations. Sapsuckers, on the other hand, are adapted to tolerating and coping with their squirrel neighbors.

As a resident species seeking a nest tree in March before arrival of the migratory sapsuckers, Hairy Woodpeckers might take over a *Fomes*-infected aspen already in use were it not for the tree being occupied by flying squirrels. The squirrels would then be a factor favorable to the sapsuckers in preserving a nest aspen against what might otherwise be a closely competing species of woodpecker. In any event, I have never found a Hairy Woodpecker even attempting to excavate an aspen used by sapsuckers in previous years.

In conclusion it might be noted that while much is owed to Haartman (1957) for his discussions on adaptations in hole-nesting birds and to Nice (1957) for her findings that 65 per cent of eggs resulted in fledglings among hole-nesters as compared to 43 per cent for open nesters, neither

of these authors included woodpeckers among the species studied. Woodpeckers should in many ways be considered in a separate category. They select trees in which to excavate rather than nest holes already built and while some species such as the Hairy Woodpecker do have to compete with both avian (Starlings) and mammalian (flying squirrel) competitors, sapsuckers appear to face almost no competition of this type whatever. The selection pressures which may have led to the evolution of their search image of the safest and most secure type of nest tree may have consisted largely of that highly versatile predator, the raccoon, as well as of other factors as varied as carpenter ants whose presence might never be suspected in a tree unless one examined a nest aspen by cutting it down and sectioning it with a power saw. There is obviously, in this regard, much to be learned about the adaptations of sapsuckers and other woodpeckers which enable them to survive as hole-nesting species.

SUMMARY

An hypothesis arising from present studies is that Yellow-bellied Sapsuckers have a search image of aspens having straight boles and diameters of 20 to 25 centimeters as being optimal nest sites when they bear mature conks of *Fomes igniarius*. This fungus also attacks the heartwood of other trees. When butternuts are infected they may be as suitable for nesting as aspens in providing a tough living shell of sapwood surrounding a center of soft decay which can be excavated readily. Such trees offer maximal, although not always complete, protection against raccoons which appear to be the main predators. Raccoons may leave a characteristic circle of superficial tooth marks in unsuccessful attacks on nest entrances but several examples are given where they succeeded, after persisting efforts, in dragging sapsuckers out through undamaged entrance holes, as evidenced by piles of feathers on the ground below. The nest sites involved were either too near the ground or possibly too shallow.

Sapsuckers, unlike other species of eastern woodpeckers, have a habit of re-using suitable nest trees, making fresh excavations each year and in some *Fomes*-infected aspens, for periods of 6 or 7 years. Such trees come to resemble tenement houses with the old nest holes being not infrequently occupied by flying squirrels. Yellow-bellied Sapsuckers appear to be well adapted to living in the close presence of squirrels and this may give them a competitive advantage in relation to Hairy Woodpeckers which can, under some circumstances, seek the same type of a nest tree.

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