HEARTWOOD DECAY AND VERTICAL DISTRIBUTION OF RED-NAPED SAPSUCKER NEST CAVITIES

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ABSTRACT.—This paper describes a dynamic spatial pattern of Red-naped Sapsucker (*Sphyrapicus nuchalis*) cavity excavation in aspen groves and evaluates the possible importance of heartwood decay distribution, a prerequisite for nest excavation, in producing it. Sapsuckers typically situate the first cavity excavation in a tree relatively close to the ground and then make progressively higher excavations in subsequent years. Heartwood decay is reported to infect aspen via the roots or broken branch stubs, mostly at the base of the trees. Coring revealed that all nest trees were rotted at the base. The pattern of sapsucker cavity excavation can be explained as the outcome of an interaction between the distribution over height within trees of both heart rot and predation risk. *Received 21 Oct.* 1992, accepted 14 May 1993.

Species interactions involving the Red-naped Sapsucker (Sphvrapicus nuchalis; hereafter sapsucker) may exert a significant influence on community structure. The local distributions and abundances of several secondary cavity nesting birds are enhanced by old sapsucker nest cavities (Daily et al. 1993). Similarly, many organisms benefit from the rich sap resources tapped by the sapsucker (e.g., Kilham 1953, 1958; Ehrlich and Daily 1988). What factors, in turn, influence the distribution of the sapsucker? Heartwood decay is known to be an important precursor to nest cavity excavation for sapsuckers and other woodpeckers (e.g., Bent 1939, Conner et al. 1975, Conner et al. 1976). Throughout their range, sapsuckers are reported to nest in trees that are susceptible to heart rot, including aspen (*Populus tremuloides*), birch (*Betula spp.*), and cottonwood (Populus spp.) (Erskine and McLaren 1972, McClelland and Frissell 1975, Keisker 1987). They show a strong preference for nest trees that possess indicators of heartwood decay, such as evidence of past injury and fungal fruiting bodies (conks) (Keisker 1987). The distribution of fungi that cause heartwood decay, therefore, may influence the occurrence of sapsuckers on micro- and local scales. Here I describe a dynamic spatial pattern of sapsucker cavity excavation in aspen, whereby typically the first excavation in a tree is situated relatively low and is followed by progressively higher excavations in subsequent years. I evaluate the possible importance of the distribution of heartwood decay (principally Fomes igniarius var. populinus) in producing this pattern.

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METHODS

Data were gathered in the vicinity of the Rocky Mountain Biological Laboratory (RMBL, 2900 m elevation) in Gunnison County, Colorado. A total of 33 active Red-naped Sapsucker nests were located during the 1987–1991 breeding seasons in 26 different quaking aspen (*Populus tremuloides*) trees. Diameter at breast height (dbh), condition (dead or live) of the nest tree, cavity height, and total number of cavities per tree were recorded.

Most (21/26) nest trees were cored at 0.5 m height to determine whether heart rot was present. The aspen tree of similar dbh closest to the nest tree was also cored (in all cases but one). Finally, 160 randomly selected aspen trees (of dbh > 16 cm) within a 3 km radius of RMBL were cored. All trees were cored at the base (0.5 m height), and an additional second core at 4.5 m height was taken from 20 trees without nest cavities.

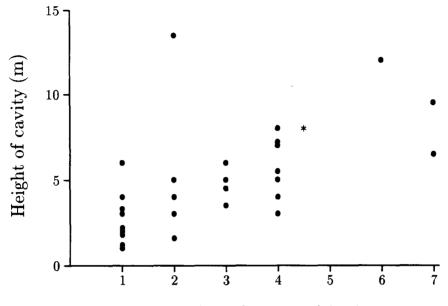
Core condition was evaluated on the basis of color, structural integrity, and ease of extraction. Cores were scored as "not rotted" (where no difference in color, structural integrity, or ease of extraction between the heartwood and sapwood was evident), "rotted" (where the heartwood was discolored, crumbly, dry, and more easily extracted relative to the sapwood), or "intermediate" (where the heartwood was discolored but not yet dry or crumbly).

RESULTS

Cavity location.—All but three active sapsucker nests were freshly excavated during the season of use (cf Short 1979); most of the nests (91%; 30/33) were in live trees. The majority of nests (67%; 22/33) were situated in trees bearing nest cavities excavated during previous years (cf Flack 1976).

The height of active nest cavities was positively correlated with the number of other cavities already present in nest trees (Fig. 1; r = 0.62, P < 0.01). Where there was more than one cavity in a tree, the active sapsucker nest was in the highest position 86% of the time (18/21; $\chi^2 = 22.46$, df = 6, P < 0.001), and was never in the lowest cavity. The mean height of active nest cavities located in trees with no other cavities (2.7 \pm 0.8 m, N = 11) was significantly lower than the mean height of active nests in trees with more than one cavity (6.0 \pm 0.6 m, N = 22; ANOVA, $F_s = 12.44$, df = 31, P < 0.005). Nonetheless, active cavities were concentrated at the lower range of heights (test for skewness, $g^1 = 1.2081$, $t_s = 2.9564$, df = ∞ , P < 0.01).

Distribution of heartwood decay. —All 21 cored nest trees were rotted at the base, compared to only 40% (8/20) of trees adjacent to nest trees (G-test, G(William's) = 21.640, df = 1, P < 0.001, N = 41 trees). In the broad survey of the condition of the bases of mature aspens, 15% (24/ 160) were rotted, 5.6% (9/160) were at an intermediate stage of heartwood decay, and 79% (127/160) were not rotted at the base. Of the 20 aspens that I cored both at 0.5 and at 4.5 m heights, 3 (15%) were rotted at both heights, 1 (5%) showed intermediate rot at the base and none at 4.5 m, and 16 (80%) were not rotted at either height. Trees adjacent to infected



Total number of nest cavities in tree

FIG. 1. The heights of active nest cavities are plotted as a function of the total number of cavities in the tree (r = 0.619; P < 0.01). The asterisk refers to a tree where it was unclear whether the highest cavity had actually been fully excavated and used for nesting.

nest trees had a slightly higher probability of bearing indications of heartwood decay (at the base) than trees in the random sample (0.40 vs 0.21; G(William's) = 3.256, df = 1, P < 0.10, N = 180 trees).

DISCUSSION

Sapsuckers tend to excavate the first cavity in previously unexcavated trees at a relatively low height and in subsequent years excavate new nest cavities above all older cavities. Trunk diameter did not appear to be an important factor in producing this pattern. Aspen trunks taper gradually, and all nest trees were estimated to be at least 15 m high. If trunk diameter were the principal constraint, one would expect a normal distribution of cavity heights, truncated at the greater heights where the trunk narrows. In fact, the distribution was skewed in the reverse direction: twenty-three (of 33) active nest cavities were situated less than 6 m from the ground. The inclusion of old nest cavities (of unknown species origin) in this analysis would have skewed the distribution considerably more as the active nests were nearly always the highest.

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A possible explanation of the pattern of nest excavation is suggested by the vertical distribution of heartwood decay. The shelf fungus (*Fomes igniarius* var. *populinus*) is the principal cause of heart rot in aspens throughout its range (Basham 1958). Trees are most prone to infection by this fungus (and a variety of others) through the roots and through dead, broken branch stubs or sites of injury (Basham 1958, Shigo 1965), which are concentrated in the lower part of aspen trunks (pers. obs.). All nest trees were rotted at the base, and no trees were found with heart rot above an unrotted section of trunk. This contrasts with the general finding that woodpeckers excavate cavities in trees where the mode of entry of heartwood decay is through upper broken branch stubs (Conner et al. 1976, Conner and Locke 1982).

If most aspen are first infected at or near the base of the tree, then the decayed heartwood would taper in diameter with height from the base. This suggests that the diameter of the decay column may be a limiting factor on sapsucker nest excavation. I hypothesize that sapsuckers make the first cavity excavation in a tree near the base because the probability of encountering heartwood decay of sufficient diameter is highest there. Under this hypothesis, the optimal location of subsequent cavity excavation attempts is determined by the relative probabilities of encountering a suitable decay column just above the old cavity versus in an unexcavated tree.

If the probability of encountering sufficient heart rot is highest at the base of aspen trees, why do sapsuckers situate cavities in progressively higher parts of the same tree even when there is ample room below old cavities? Predation risk could be the explanation. Maximizing the probability of encountering sufficient heart rot diameter in an unexcavated tree involves a trade-off with a higher risk of predation associated with low cavities. The Red-naped Sapsucker and other woodpeckers, including the Northern Flicker (*Colaptes auratus*), the Red-headed Woodpecker (*Melanerpes erythrocephalus*), and the White-headed Woodpecker (*Picoides albolarvatus*), sometimes excavate nest cavities very close to the ground where they may be vulnerable to non-arboreal predators, including carpenter ants (*Camponotus* spp.) (Bent 1939, Keisker 1987, Kilham 1971, Short 1982).

In this study, a weasel (*Mustela* sp.) was observed preying upon the nest of a banded male that had successfully fledged young from nests in two nearby trees in previous seasons. The cavity was at 1.2 m height in an aspen with no other nest cavities. The tree was sectioned into several meter-length segments in order to determine the condition of the trunk. It showed heartwood decay extending from the base to a height of about 9 m, of sufficient diameter to have allowed excavation of a cavity nest at

least 5 m above the chosen height. Thus, while sapsuckers most likely can detect the presence of heartwood decay prior to drilling, they may be unable to assess the diameter of the decay column.

In conclusion, I propose that the dynamic pattern of sapsucker nest cavity excavation is the outcome of an interaction between the distribution of both heart rot and predation risk. Furthermore, the tendency for sapsuckers to nest in the same cluster of a few trees over time (Kilham 1971, pers. obs.) may be explained partly by the higher probability of encountering heart rot in trees near former nest trees than at random.

An earlier study showed that the local distribution of sapsuckers is restricted to areas where willow (*Salix* spp.) and aspen cooccur in close proximity (Daily et al. 1993). The interactions between willow, aspen, heart rot fungi, and sapsuckers may affect other species by influencing, for example, the nest proximity of secondary cavity nesters and social, predatory, and other interactions between them. This work highlights the potential importance of subtle species interactions in structuring biological communities.

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