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DOES TREE HARDNESS INFLUENCE NEST-TREE SELECTION BY PRIMARY CAVITY NESTERS?

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ABSTRACT.—Cavity-nesting birds that excavate nest holes may be limited by the availability of suitable substrates for excavation. Suitability of trees for excavation may be influenced by substrate hardness and excavation strength of the bird. Excavation strength, in turn, may vary among bird species, causing nest-tree selection to vary among excavator species. We examined use of quaking aspens (*Populus tremuloides*) for nest trees as a function of tree hardness in four species of woodpeckers: Williamson's Sapsucker (*Sphyrapicus thyroideus*), Red-naped Sapsucker (*S. nuchalis*), Downy Woodpecker (*Picoides pubescens*), and Hairy Woodpecker (*P. villosus*). Hardness of trees was measured at 95 nest trees, 94 neighboring trees, and 150 random trees using a new technique described here. Other investigators have speculated that the gross external appearance of trees/snags can be used to estimate hardness. Hardness decreased from live trees to partly dead trees to dead trees and with increasing height in trees, but hardness was not related to other external features such as numbers of conks or percentage of the tree covered with bark. All four bird species chose nest trees that were softer than neighboring or random trees, and nest trees were softer at nests than at other heights measured. The four species selected trees of different hardness for nesting; Red-naped Sapsucker and Hairy Woodpecker chose harder trees than Williamson's Sapsucker and Downy Woodpecker. These results suggest that primary cavity nesters are sensitive to subtle characteristics of trees that reflect hardness, some of which may not be apparent in the external appearance of the trees. *Received 24 January 1997, accepted 12 November 1998.*

CAVITY-NESTING BIRDS that do not excavate their nest holes (i.e. secondary cavity nesters) are commonly limited by the availability of nest sites (von Haartman 1957, Brush 1983, Brawn et al. 1987, Brawn and Balda 1988, Gustafsson 1988). Excavating species also may be limited by the availability of nest sites because they are thought to require tree species or tree types (e.g. older, diseased, dead, or dying) with soft wood, and such trees may be limited in availability (Kilham 1971; Conner et al. 1975, 1976; Crockett and Hadow 1975; McClelland and Frissell 1975; Raphael and White 1984; Runde and Capen 1987; Daily 1993). However, the degree of softness required for excavation is unclear. Excavating bird species may differ in excavation abilities related to their morphology and behavior, which could cause variation among species in hardness of wood selected for excavation (Lawrence 1967, Bock 1970, Miller and Bock 1972, Kilham 1979, McClelland et al. 1979, Martin 1993). Indeed, variation in excavation or hammering strength is thought to be related to the morphological attributes of species (Burt 1930, Spring 1965, Kirby 1980).

Species with weaker excavating abilities potentially require softer wood for excavation of nest holes; if such soft wood cannot be found, then they may have to rely on preexisting holes (Martin 1993). Excavating species vary considerably in their use of existing holes (Martin 1993). If increased dependence on existing holes reflects constraints imposed by weaker excavation morphology, then such species may face greater nest-site limitation than species that can excavate in harder wood (Martin 1993). These relationships have potential ramifications for life-history attributes because greater nest-site limitation may favor greater reproductive effort (Beissinger and Waltman 1991; Martin 1992, 1993; Martin and Li 1992), and use of softer wood may increase vulnerability to nest predators and thereby favor shorter nes-

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tling periods (Kilham 1979, Martin 1995). In addition, dependence on soft wood that is limited in availability has important implications for habitat management; identifying the extent to which soft wood is required by different bird species, and what connotes soft wood, can aid conservation programs.

Many studies have explored availability and use of soft substrates by characterizing decay in trees as evidenced by broken tops, lost limbs, *Fomes* infestation, and proportion of bark remaining (e.g. McClelland and Frissell 1975, Conner et al. 1976, Mannan et al. 1980, Cline et al. 1980, Raphael and White 1984, Swallow et al. 1986, Runde and Capen 1987, Schreiber and deCalesta 1992). Results of these studies suggest that excavating bird species choose nest substrates that differ in hardness. Yet, such approaches assume that decay classes as defined by external characteristics of trees reflect actual changes in substrate hardness without directly measuring it. Conner (1977) measured tree hardness by letting a hammer fall from a constant position and recording the number of falls required to drive a spike 4 cm into a tree. His goal, however, was to determine whether nest-entrance orientation was chosen based on tree hardness and not to determine whether bird species differed in their choice of substrates based on hardness. In addition, Conner et al. (1994) measured tree hardness using a Pilodyn®, but they examined hardness at foraging sites and not at nest trees.

We examined nest-substrate hardness within a single species of tree, quaking aspen (*Populus tremuloides*), because as a first approach it reduces the confounding factor of differences in hardness among tree species. Moreover, we focus on aspen because it is used most frequently for nesting by all excavating species on our study sites (Li and Martin 1991), as well as at other locations (e.g. Kilham 1971, Winternitz and Cahn 1980, Smith 1982, Daily 1993). Aspens are used for nests by two pairs of congeneric woodpeckers that coexist on our sites and are thought to differ in dependence on soft substrates: Red-naped Sapsucker (*Sphyrapicus nuchalis*), Williamson's Sapsucker (*S. thyroideus*), Hairy Woodpecker (*Picoides villosus*), and Downy Woodpecker (*P. pubescens*).

Various studies allow several contradicting *a priori* predictions. A morphological study by Kirby (1980) led to predictions that excavation strength increased in the order Red-naped Sapsucker < Williamson's Sapsucker < Downy Woodpecker < Hairy Woodpecker. Kilham (1979) also argued that Downy Woodpeckers depended on softer substrates than Hairy Woodpeckers. Characterization of decay classes by Raphael and White (1984), in contrast, suggested that Hairy Woodpeckers used softer substrates than either species of sapsucker. Yet, Lawrence (1967) argued that Downy Woodpeckers use much softer wood than sapsuckers, which use softer wood than Hairy Woodpeckers. Finally, Martin (1993) argued that increasing use of existing holes reflects weaker excavation abilities and a need for softer substrates, and his data predict that substrate hardness should increase in the order Williamson's Sapsucker < Downy Woodpecker < Red-naped Sapsucker < Hairy Woodpecker. Thus, morphological predictions (Kirby 1980) differ from those based on more standard decay classes (Raphael and White 1984) or use of existing holes (Martin 1993). Here, we describe a method for measuring substrate hardness and test these alternative predictions.

STUDY AREA AND METHODS

Our study took place on the Mogollon Rim in central Arizona during the breeding seasons of 1994 and 1995. Study sites were high-elevation (2,600 m) forest drainages of mixed conifer and deciduous canopy species. Dominant trees included ponderosa pine (*Pinus ponderosa*), quaking aspen, Douglas-fir (*Pseudotsuga menziesii*), southwestern white pine (*Pinus strobiformes*), white fir (*Abies concolor*), and Gambel oak (*Quercus gambelii*). New Mexico locust (*Robinia neomexicana*), canyon maple (*Acer grandidentatum*), and young canopy trees dominated the understory (see Martin 1988, 1998). Sixteen species of cavity-nesting birds breed on the sites (Martin 1988).

All four species of woodpeckers that we studied excavate nests in quaking aspen more frequently than in any other available substrate (Li and Martin 1991). Therefore, tests were restricted to aspen trees. We searched for nests in 17 snow-melt drainages. We used only nests in which egg laying was completed and incubation was initiated to avoid possible differences in trees with incomplete excavations.

We looked at eight nest-tree characteristics: health, hardness, diameter at breast height (dbh), tree height, number of cavities, number of fungal conks (*Fomes*), height of cavity (on nest trees), and percentage of bark. We categorized the health of trees in three classes that were typical of those used in previous studies: "live" consisted of trees in which all

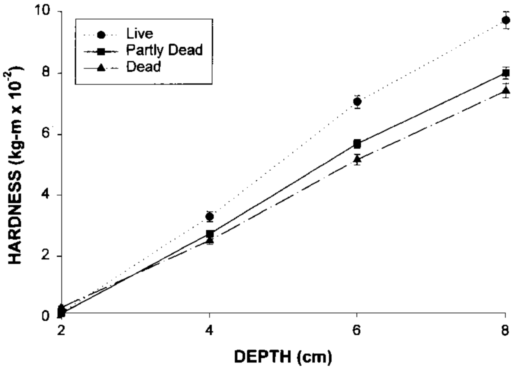

FIG. 1. Tree hardness at increasing depth into the sapwood for randomly sampled aspens of three health classes. Data are marginal means ($\bar{x}$ ± SE) from ANOVA that included number of conks, number of cavities, percentage of tree with bark, and dbh as covariates and tree height and use classes as additional main effects.

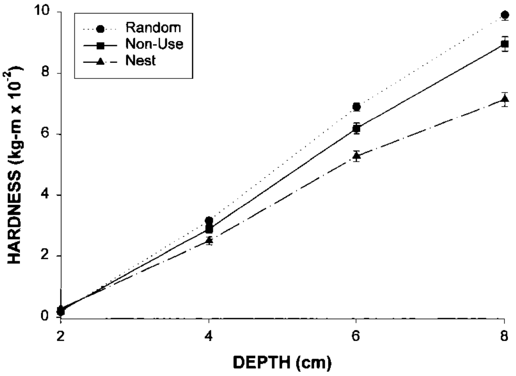

FIG. 2. Tree hardness at increasing depth into the sapwood for aspens of different use classes. Data are marginal means ($\bar{x}$ ± SE) from ANOVA that included number of conks, number of cavities, percentage of tree with bark, and dbh as covariates and tree height and health classes as additional main effects.

branches had leaves; "partly dead" consisted of trees with some (>1) dead branches, but at least one live branch; and "dead" included trees or snags that were completely dead. Percentage of bark was described by ocular estimation. Total numbers of cavities and fungal conks were counted for each tree. We estimated tree height using a clinometer and measured dbh using a diameter stick.

We sampled nest trees, neighboring trees, and random trees. "Nest trees" were trees that had active nests of the study species. We sampled as many nest trees as we could find in the two field seasons of the study. "Neighboring trees" were trees that were paired with nest trees, and each was the closest neighbor to the nest tree that was of the same health (i.e. live, partly dead, or dead) and size class as the nest tree. Finally, "random trees" were chosen in each plot by the following method: plots were staked at 25-m intervals, and every other stake (every 50 m) was used as the sampling point from which the nearest fully grown (>20 m tall) aspen of each health class that was >15 cm dbh was then sampled. In total, we tested 150 random trees (50 live, 50 partly dead, and 50 dead). Random trees were restricted to trees that lacked an active woodpecker nest. When any of the selected trees had an active nest, the next-closest tree of the same health class that did not contain an active woodpecker nest was selected. After the young had fledged from the nests, we sampled the 95 nest trees and 94 corresponding neighboring trees (in one case, a neighboring tree was unavailable within 100 m of the nest tree).

Hardness was tested using a ¼-inch-diameter lag bolt and a torque wrench based on a method developed by S. Lohr. Previous studies have examined hardness based on one blow into a tree (e.g. Conner 1977, Conner et al. 1994), which assumes that hardness at the exterior is linearly related to hardness in the interior across trees. However, we wanted to examine whether hardness increases in a nonlinear fashion with depth, and whether that relationship differs among tree types. If some trees are harder at the exterior but softer in the interior than other trees, the hard exterior would produce biased results if based on a single reading starting from the exterior as conducted previously. Thus, we took torque readings (in kg-m) at depths of 2, 4, 6, and 8 cm to measure hardness at increasing depths and found that, in fact, dead trees tended to have a harder exterior (the wood dried out) than partly dead or live trees (see Fig. 1), which justified our approach of measuring multiple depths. We sampled nest trees and neighboring trees at four heights (1, 5, and 8 m, as well as 2 to 3 cm above the nest) using Swedish climbing ladders. We sampled random trees only at 1, 5, and 8 m because random trees had no corresponding nest height. We sampled different heights because some authors (e.g. Daily 1993) have argued that sapsuckers dig progressively higher nest holes as *Fomes* infection increases upward on the tree, suggesting that lower heights are softer.

Absolute torque readings increase with depth because they are influenced by hardness at the previous depth, so we used repeated-measures analysis of variance, with depth as the repeated measure, to analyze differences in hardness among main effects. In all cases, the within-subject factor (depth) was always highly significant (i.e. hardness increased with depth; see Figs. 1–4); because we were more concerned with differences in this effect among subjects, we report only the among-subject results. We examined four main effects: bird species, tree health, sampling height, and tree use (i.e. nest, neighbor,

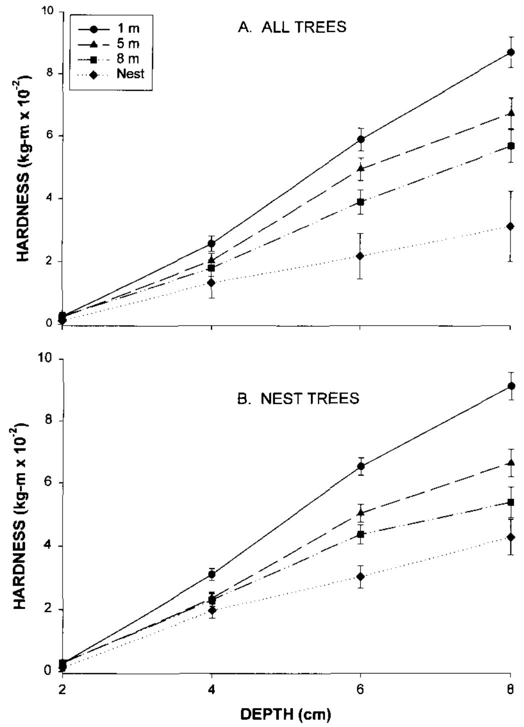

FIG. 3. Tree hardness at increasing depth into the sapwood for aspens of different heights; (A) all trees, (B) nest trees only. Data are marginal means ($\bar{x}$ ± SE) from ANOVA that included number of conks, number of cavities, percentage of tree with bark, and dbh as covariates and use classes and health classes as additional main effects.

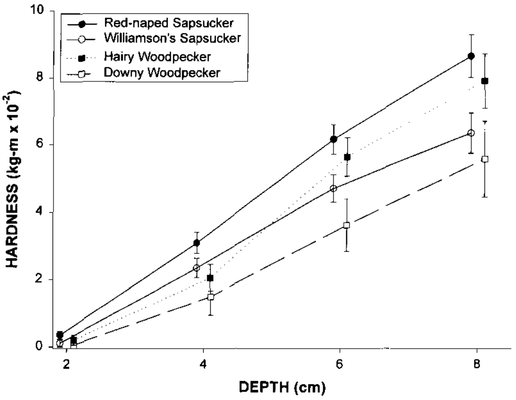

FIG. 4. Tree hardness at increasing depth into the sapwood for aspens among four bird species. Data shown are marginal means ($\bar{x}$ ± SE) from ANOVA that include number of conks, number of cavities, percentage of tree with bark and dbh as covariates, and sampling height and health classes as additional main effects.

random). In some cases, all four main effects could not be examined because bird species could not be tested for random trees. In these cases, only three main effects were tested. By including all main effects possible, in essence we nested effects within each other and eliminated possible pseudoreplication while taking advantage of the error variance gained by repeated sampling at different heights and depths. For example, height was always included as a factor because we sampled trees at multiple heights, and inclusion of height as a factor then tested differences in hardness among other factors controlled for height but included the error variance among heights. As a further check, we conducted an ANOVA on health and use classes for a single height (5 m, which was used because we had complete samples at this height) and a single depth (8 cm, which integrated all previous depths). We also conducted an ANOVA on health, use, and height for a single depth (8 cm). Finally, we examined differences among bird species and use classes for nest and neighbor trees at a single height (5 m) and a single depth (8 cm). All of these analyses eliminated any replicated sampling within a single tree, and all produced the same results that we found with repeated-measures ANOVA; to keep the results concise, we report only the repeated-measures ANOVA because we believe we gain additional information by examining relationships across depth and height classes. Diameter at breast height, number of cavities, number of fungal conks, and percent bark were examined as possible covariates in all cases, including single depth and height analyses. In some cases, interactions between main effects in the repeated-measures ANOVA were significant such that the slope for hardness by depth differed among bird species, height, and health classes. However, in every case, general significance and ranking of hardness among bird species, height, and health classes did not differ when examined separately. Because of this lack of difference, we present only the overall analyses rather than repeating analyses for each main effect within every level of every other main effect. The resulting figures that we present are based on marginal means that control for all other main effects and covariates, because these are the values that we compared in our analyses.

RESULTS

The percentage of a snag covered by bark is thought to reflect decay, and cavity-nesting birds have been found to choose conifer snags with greater bark cover (Cline et al. 1980, Raphael and White 1984, Schreiber and deCalesta 1992; but see Scott et al. 1978). The percentage

TABLE 1. Characteristics of trees ($\bar{x}$ ± SE) in three health classes.

Variable	Health class		
	Live	Partly dead	Dead
Bark coverage (%)	98.2 ± 2.68	97.6 ± 2.13	48.7 ± 2.01
No. of cavities	0.58 ± 0.19	0.89 ± 0.15	1.73 ± 0.14
No. of conks	6.75 ± 0.76	8.26 ± 0.60	2.67 ± 0.57
Hardness (kg-m)	75.3 ± 2.84	59.1 ± 2.24	51.8 ± 2.11

of a tree covered by bark was correlated with hardness ($r = 0.179$, df = 4 and 337, $P = 0.003$) across all aspen trees, but it explained only a small portion (3.2%) of the variation in hardness. The relationship was positive and reflected the greater bark covering of live trees, which are harder. When we restricted the analysis to snags, the percentage of a snag covered by bark was not correlated with hardness ($r = 0.005$, df = 4 and 337, $P = 0.96$). Percentage bark cover differed among health classes ($F = 177.0$, df = 2 and 344, $P < 0.001$), with almost complete bark coverage on live and partly dead trees and only about 50% coverage on dead trees (see Table 1).

The presence of conks often is used as a measure of decay (e.g. Conner 1978, Runde and Capen 1987). The number of conks was negatively correlated with hardness ($r = -0.168$, df = 4 and 337, $P = 0.002$) when examined across all trees, but again, it explained only a small portion (2.8%) of the variation in hardness. The number of conks has been used to estimate decay and heart rot in live and partly dead trees. When we restricted our analysis to these two classes of trees, the number of conks was more strongly correlated with hardness ($r = -0.252$, df = 4 and 200, $P < 0.001$), but it still explained only a small portion (6.3%) of the variation in hardness. The number of conks differed among health classes ($F = 24.4$, df = 2 and 338, $P < 0.0001$), being highest in partly dead trees but lowest in dead trees (Table 1), which does not support the notion that conks are a clear measure of decay or hardness.

Harder trees generally had fewer cavities ($r = -0.216$, df = 4 and 337, $P < 0.001$), which was reflected by differences in the number of cavities among health classes; the number of cavities increased from live to dead trees ($F = 14.7$, df = 2 and 344, $P < 0.0001$), and hardness decreased from live to dead trees ($F = 22.0$, df = 2 and 343, $P < 0.0001$; see Table 1).

Main effects of tree health (live, partly dead, dead), tree use (random, neighbor, nest), and sampling height (1, 5, 8, and nest height), plus all covariates (number of conks, number of cavities, percentage of tree with bark, and dbh) were analyzed simultaneously across all data (random, neighbor, and nest). All three main effects were statistically significant, whereas none of the covariates was significant, although number of conks showed a marginally significant tendency to increase with decreasing hardness ($F = 3.3$, $P = 0.068$). Tree hardness differed among health classes ($F = 14.1$, df = 2 and 1,019, $P < 0.0001$), with live trees being harder than partly dead trees, which were harder than dead trees (Fig. 1); this pattern held within each use and height class. Tree hardness also differed among use classes ($F = 21.6$, df = 2 and 1,019, $P < 0.0001$), with randomly sampled trees being harder than neighboring trees, which were harder than nest trees (Fig. 2); this pattern was consistent among health and height classes. Finally, tree hardness differed among sampling heights ($F = 26.9$, df = 3 and 1,018, $P < 0.001$), with hardness decreasing with sampling height and trees being softest at the height of the nest (Fig. 3A). Nests generally were higher than the other sampling heights, with nests averaging between 11 and 17 m across woodpecker species. Nest heights averaged 11.6 ± SE of 0.25 m for Williamson's Sapsucker, 12.6 ± 0.24 m for Red-naped Sapsucker, 14.9 ± 0.65 m for Downy Woodpecker, and 17.1 ± 0.65 m for Hairy Woodpecker. Hardness differed strongly among heights within nest trees alone ($F = 19.5$, df = 3 and 317, $P < 0.0001$), decreasing with height and being softest at the height of the nest (Fig. 3B).

Tree hardness differed among bird species ($F = 6.4$, df = 3 and 611, $P < 0.0001$) within height and use classes (Fig. 4). In particular, nest trees were harder for Red-naped Sapsucker than for Williamson's Sapsucker (Duncan's test, $P < 0.01$) and for Hairy Woodpecker than for Downy Woodpecker ($P < 0.01$; see Fig. 4).

When hardness was examined at a single depth (8 cm) and height (5 m), species differed from each other ($F = 2.8$, df = 3 and 181, $P = 0.04$) but in a slightly different order; Williamson's Sapsucker used the softest trees ($\bar{x} = 44.8 \pm 3.4$), followed by Downy Woodpecker (54.5 ± 7.3), Red-naped Sapsucker (57.7 ± 3.2), and Hairy Woodpecker (64.6 ± 6.6).

DISCUSSION

Hardness of trees chosen for nesting clearly differed among bird species and differed from neighboring and random trees. However, hardness did not differ among bird species as predicted by morphological studies. Sapsuckers were predicted to have weaker excavating morphology and to choose softer trees than would species of *Picoides* (Burt 1930, Spring 1965, Kirby 1980). Instead, we found that the Downy Woodpecker chose particularly soft nesting substrates and softer substrates than either species of sapsucker or the Hairy Woodpecker; these results are consistent with other field observations (Lawrence 1967, Conner et al. 1975, Kilham 1979). Moreover, Red-naped Sapsuckers chose trees that were harder than those chosen by either of the *Picoides* species (see Fig. 4). These patterns conflict with predictions from morphological studies, but all three morphological studies predicted hardness preferences based on extent of diet that depended on wood-boring insects. Foraging habits in general, and foraging by "woodpecking" in particular, may not provide generally accurate representations of the ability of species to excavate nest holes. Thus, earlier morphological estimates of excavation strength may be based on weak and sometimes incorrect assumptions.

Predictions were fairly accurate when based on percentage of nests placed in existing holes under the assumption that greater use of existing holes reflects increasing need for a soft substrate (Martin 1993). Use of existing holes is greater for Downy Woodpeckers than for Hairy Woodpeckers (Martin 1993), and Downy Woodpeckers chose trees that were softer (Fig. 4). Similarly, Williamson's Sapsucker use existing holes more often than Red-naped Sapsuckers (Martin 1993), and Williamson's Sapsuckers chose softer trees (Fig. 4). Thus, predictions within each genus based on use of existing holes were supported, but predictions between genera were only partly accurate. On the other hand, when we examined hardness at a single height and depth, the order within and among genera was exactly as predicted (see Results). A larger sample of species is needed to more fully examine this issue. Nonetheless, predictions of nest-tree hardness based on use of existing holes were more accurate than those based on morphology, suggesting that broader biomechanical studies are needed.

Hardness was partly reflected by decay class; live trees were harder than partly dead trees, which were harder than dead trees (Table 1, Fig. 1). However, the difference in hardness between partly dead trees and dead trees was not nearly as large as that between partly dead trees and live trees, indicating that tree hardness is not linearly related to tree health. Moreover, differences among decay (or health) classes were not nearly as great as differences among use classes or height, indicating that decay class is a reasonably weak indicator of hardness. In addition, neither percentage of the tree covered with bark nor number of conks was a good predictor of tree hardness for aspens. These features are commonly used to assess tree condition, but for aspens, external characteristics do not effectively reflect subtle changes in hardness that appear to be recognized by birds in their selection of nest trees.

Finally, nest-tree hardness declined with increasing height (Fig. 3). Similarly, Conner et al. (1994) found that hardness of trees used by foraging woodpeckers declined with height for three of four height classes, with the lowest class being softer than expected for its height. Both of these results do not support Daily's (1993) speculation that aspens decay in an upward progression (i.e. upper parts are harder) or that sapsuckers shift nest sites continuously upward among years. Moreover, we found that nest holes could be higher or lower in succeeding years (pers. obs.), and Conner et al. (1975) found that decay and nest sites of Pileated Woodpeckers (*Dryocopus pileatus*) moved down among years. Regardless of the direction of decay, birds appear to be choosing both a height of the tree that is particularly soft and trees that are softer than randomly available. Conner et al. (1994) found that trees that were chosen most frequently by foraging woodpeckers were softer than trees that were chosen less often. Ultimately, these results suggest that soft substrates are important to excavating and foraging woodpeckers and are more important for some species than for others; some species, such as Downy Woodpecker and Williamson's Sapsucker, seem to require softer wood for excavation than do congeners

The availability of these particularly soft trees is limited in the forests where we worked, as exemplified by the general hardness of randomly sampled trees. Studies of woodpeckers in other locations have found that some species interact aggressively with other cavity-nesting species and that nest usurpation can occur among species (Ingold 1989, Kerpez and Smith 1990, Rendell and Robertson 1991), further suggesting that nest sites are limited for excavating birds. Maintenance of dead trees for as long as possible to allow them to continue to decay and soften is needed. In addition, many of these species of woodpeckers seem to prefer nest trees that are surrounded by a patch of other relatively soft trees, possibly to ensure available sites for future nesting, or reflecting that decay tends to be site specific rather than tree specific. In either case, the results suggest that patches of soft trees (e.g. old snags or *Fomes*-infected live trees) are needed to maintain populations of cavity nesters (see Swallow et al. 1986, Li and Martin 1991, Conway and Martin 1993). Our data are from a single species of tree in one location; consequently, studies of hardness relationships are needed for more species of trees and birds from a variety of locations to ascertain general patterns. The clear differences that we found suggest that much can be gained by this approach.

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LITERATURE CITED

BEISSINGER, S. R., AND J. R. WALTMAN. 1991. Extraordinary clutch size and hatching asynchrony of a Neotropical parrot. Auk 108:863–871.

BOCK, C. E. 1970. The ecology and behavior in the Lewis Woodpecker (*Asyndesmus lewis*). University of California Publications in Zoology 92:1–100.

BRAWN, J. D., AND R. P. BALDA. 1988. Population biology of cavity nesters in northern Arizona: Do nest sites limit breeding densities? Condor 90: 61–71.

BRAWN, J. D., W. J. BOECKLEN, AND R. P. BALDA. 1987. Investigations of density interactions among breeding birds in ponderosa pine forests: Correlative and experimental evidence. Oecologia 72:348–357.

BRUSH, T. 1983. Cavity use by secondary cavity-nesting birds and response to manipulations. Condor 85:461–466.

BURT, W. H. 1930. Adaptive modifications in the woodpeckers. University of California Publications in Zoology 32:455–524.

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

CONNER, R. N. 1977. The effect of tree hardness on woodpecker nest entrance orientation. Auk 94: 369–370.

CONNER, R. N. 1978. Snag management for cavity-nesting birds. Pages 120–128 *in* Proceedings of the workshop: Management of southern forests for nongame birds (R. M. DeGraaf, Ed.). United States Forest Service General Technical Report SE-14.

CONNER, R. N., R. G. HOOPER, H. S. CRAWFORD, AND H. S. MOSBY. 1975. Woodpecker nesting habitat in cut and uncut woodlands in Virginia. Journal of Wildlife Management 39:144–150.

CONNER, R. N., S. D. JONES, AND G. D. JONES. 1994. Snag condition and woodpecker foraging ecology in a bottomland hardwood forest. Wilson Bulletin 106:242–257.

CONNER, R. N., O. K. MILLER, AND C. S. ADKISSON. 1976. Woodpecker dependence on trees infected by fungal heart rot. Wilson Bulletin 88:575–581.

CONWAY, C. J., AND T. E. MARTIN. 1993. Habitat suitability for Williamson's Sapsuckers in mixed conifer forests. Journal of Wildlife Management 57: 322–328.

CROCKETT, A. B., AND H. H. HADOW. 1975. Nest site selection by Williamson's and Red-naped sapsuckers. Condor 77:365–368.

DAILY, G. C. 1993. Heartwood decay and vertical distribution of Red-naped Sapsucker nest cavities. Wilson Bulletin 105:674–679.

GUSTAFSSON, L. 1988. Inter- and intraspecific competition for nest holes in a population of the Collared Flycatcher *Ficedula albicollis.* Ibis 130:11–16.

INGOLD, D. J. 1989. Nesting phenology and competition for nest sites among Red-headed and Red-bellied woodpeckers and European Starlings. Auk 106:209–217.

KERPEZ, T. A., AND N. S. SMITH. 1990. Competition between European Starlings and native woodpeckers for nest cavities in saguaros. Auk 107: 367–375.

KILHAM, L. 1971. Reproductive behavior of Yellow-bellied Sapsuckers. I. Preference for nesting in *Fomes*-infected aspens and nest hole inter-relations with flying squirrels, raccoons, and other animals. Wilson Bulletin 83:159–171.

KILHAM, L. 1979. Three-week vs 4-week nestling periods in *Picoides* and other woodpeckers. Wilson Bulletin 91:335–338.

KIRBY, V. C. 1980. An adaptive modification in the ribs of woodpeckers and piculets (Picidae). Auk 97:521–532.

LAWRENCE, L. de K. 1967. A comparative life-history study of four species of woodpeckers. Ornithological Monographs No. 5.

LI, P., AND T. E. MARTIN. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108:405–418.

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

MARTIN, T. E. 1988. Habitat and area effects on forest bird assemblages: Is nest predation an influence? Ecology 69:74–84.

MARTIN, T. E. 1992. Interaction of nest predation and food limitation in reproductive strategies. Current Ornithology 9:163–197.

MARTIN, T. E. 1993. Evolutionary determinants of clutch size in cavity nesting birds: Nest predation or limited breeding opportunities? American Naturalist 142:937–946.

MARTIN, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. Ecological Monographs 65:101–127.

MARTIN, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? Ecology 79:656–670.

MARTIN, T. E., AND P. LI. 1992. Life history traits of open- versus cavity-nesting birds. Ecology 73: 579–592.

McCLELLAND, B. R., AND S. S. FRISSELL. 1975. Identifying forest snags useful for hole-nesting birds. Journal of Forestry 73:414–417.

McCLELLAND, B. R., S. S. FRISSELL, W. C. FISCHER, AND C. H. HALVORSON. 1979. Habitat management for hole-nesting birds in forests of western larch and Douglas-fir. Journal of Forestry 77: 480–483.

MILLER, A. H., AND C. E. BOCK. 1972. Natural history of the Nuttall Woodpecker at the Hastings Reservation. Condor 74:284–294.

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

RENDELL, W. B., AND R. J. ROBERTSON. 1991. Competition for cavities among Great Crested Flycatchers, *Myiarchus crinitus,* Northern Flickers, *Colaptes auratus,* and Tree Swallows, *Tachycineta bicolor.* Canadian Field-Naturalist 105:113–114.

RUNDE, D. E., AND D. E. CAPEN. 1987. Characteristics of northern hardwood trees used by cavity-nesting birds. Journal of Wildlife Management 51: 217–223.

SCHREIBER, B., AND D. S. DECALESTA. 1992. The relationship between cavity-nesting birds and snags on clearcuts in western Oregon. Forest Ecology and Management 50:299–316.

SCOTT, V. E., J. A. WHELAN, AND R. R. ALEXANDER. 1978. Dead trees used by cavity-nesting birds on the Fraser Experimental Forest: A case history. United States Forest Service Research Note RM-360.

SMITH, K. G. 1982. On habitat selection of Williamson's and "Red-naped" Yellow-bellied sapsuckers. Southwestern Naturalist 27:464–466.

SPRING, L. W. 1965. Climbing and pecking adaptations in some North American woodpeckers. Condor 67:457–488.

SWALLOW, S. K., R. J. GUITIERRREZ, AND R. A. HOWARD. 1986. Primary cavity-site selection by birds. Journal of Wildlife Management 50:576–583.

VON HAARTMAN, L. 1957. Adaptation in hole-nesting birds. Evolution 11:339–347.

WINTERNITZ, B. L., AND H. CAHN. 1980. Nest holes in live and dead aspen. Pages 102–106 *in* Snag habitat management: Proceedings of the symposium. United States Forest Service General Technical Report RM-99.

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