for an average of 6.7 min/bout. Although some foliage was present above the nest, the female was still quite exposed to the midday sun and could be seen panting. We color-banded the male the same day. Sometime before 17 June the nest was depredated. Although the actual clutch size was not determined, incubation on 9 June meant that the clutch size probably was not >3 eggs, as Prothonotary Warbler females begin incubation once the penultimate egg is laid (Petit 1986). Average clutch size for this population is 4.6 and <10% of all clutches are ≤3 eggs (Petit 1986).

On 17 June we observed that the male had expanded his territory after three neighboring males had eased territorial defense while feeding fledglings. The expanded territory (based on the male's singing posts) included five nest boxes and encompassed an area of approximately 0.15 ha. On 26 June an unbanded female was incubating 4 eggs in a nest box located within the male's expanded territory. Although the identity of that female was not certain, the timing of clutch initiation and the fact that she was mated to the male suggest that she was his previous mate. The pair successfully fledged four young from that nest.

Measurements of the blackbird nest used by the warblers were compared with those of 20 other nearby nests of Red-winged Blackbirds, also built in buttonbushes in 1987. All measurements of the warbler nest were similar to those of blackbird nests except for inside depth, which was greater than the upper 95% confidence limit for the other 20 blackbird nests. This fact, along with the moss lining of the nest (Prothonotary Warblers use moss in their nests; Red-winged Blackbirds do not), suggests that the warblers altered the nest cup and made it deeper.

Lack of available natural cavities or nest boxes prompted use of the blackbird nest by the warblers. The question remains as to why the male would continue to defend an area that held no suitable nest sites. Possibly, the male had been "waiting" for a territory with suitable nest sites to become available, as is often the case in this population of Prothonotary Warblers (unpubl. data). Also, Prothonotary Warblers exhibit strong site tenacity (unpubl. data). If the male had nested at this site in a previous year, his tenacity could explain why he did not move elsewhere in search of cavities. When faced with severe nest-site limitation in habitat that is otherwise preferred, Prothonotary Warblers may utilize any site that adequately resembles a cavity, even if it is of lower quality, when the alternative would be to delay or forego breeding.

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Predation on overwintering wood borers by woodpeckers in clear-cut forests.—Few researchers have assessed the impact of woodpeckers on wood borers, a complex of insect species that burrow deep into the xylem of living trees and account for a $60–120 million annual loss of timber in the eastern United States (Donley and Worley 1976). In addition, few studies have discussed tree characteristics associated with locations of borers that were depredated, and no studies have assessed the impact of woodpeckers on wood borers in young, regenerating forests. This latter point is especially significant because of the contro-

versial practice of clear-cutting and its effect on management practices. The purposes of this study were to document the extent of woodpecker predation on overwintering populations of red oak borers (Coleoptera; *Enaphalodes rufulus*) inhabiting regenerating stems in clear-cuts and to characterize attack sites of depredated and nondepredated borers.

Study areas and methods.—Our two study sites, located in The Wayne National Forest, Hocking County, Ohio, had been clear-cut about 1970. The 3.1-ha plots were located within larger (10–12 ha) clear-cut areas, but were bordered on at least one side by mature deciduous woodland (Petit et al. 1985). Slopes were steep (average grade 17%) and drained by ephemeral creeks. Canopy heights averaged approximately 8 m, and the sites were dominated by red oak (*Quercus rubra*), chestnut oak (*Q. prinus*), white oak (*Q. alba*), hickories (*Carya* spp.), flowering dogwood (*Cornus florida*), and maples (*Acer* spp.). The clear-cuts had not yet undergone self-thinning as evidenced by the high density of stems (approximately 9000 stems/ha).

The red oak borer has a 2-year life cycle (Donley and Acciavatti 1980). Eggs are laid on trunk surfaces during the summer, and hosts range from saplings to mature trees. As the hatched beetle larvae burrow through bark in August and September, they extrude from their entrance holes a fine, light-colored frass composed of sawdust and feces. Frass accumulation indicates the presence of active borers. By November, larvae are about 5 mm long and overwinter in a dormant condition within a burrow (about 1 cm^3) just under the bark. The following summer, larvae grow to about 25 mm in length while they bore a 10–15 cm tunnel obliquely upward through the sapwood and heartwood. During the larvae's second winter dormant period, woodpeckers must excavate approximately 3–7 cm into the trees to extract them. During the following spring and summer, surviving larvae pupate and then hatch as flying adults. The breeding cycle is synchronous throughout any given red oak borer population, with adults emerging every other year.

Our study focused on the second overwintering period when the borers were >3 cm deep in tree boles. Thus, results of borer mortality due to woodpeckers do not assess the impact of woodpeckers over the borers' entire life cycle. However, because many species of wood borers spend much of their larval stages deep within tree trunks and branches (e.g., Hay 1968, Borror et al. 1976), this seemed to be a reasonable time to study the proficiency of woodpeckers at removing the borers.

In August 1982, active red oak borer holes were located within each clear-cut. Some trees showed evidence of more than one borer attack. We marked each hole with plastic flagging tape placed 1–2 m from the infested tree. For each attack site, we recorded height above ground, diameter of trunk at the attack site, and direction (N, NE, E, etc.) on the tree bole. We searched for signs of woodpecker predation during the first week of April 1983. Woodpeckers dig characteristic conical holes when attempting to excavate borers (Hay 1972).

Differences in characteristics of trees with depredated and nondepredated borers were analyzed with *t*-tests, for diameter of the tree at a borer attack site and height of an attack, and with chi-square contingency tests for orientations of borers excavated on tree trunks.

Results.—Of 234 red oak borer attack sites located 10 to 456 cm above the ground, woodpeckers excavated 11 borers on each of the two plots (7.4% and 12.8% predation). These rates were not significantly different. Percentages of marked trees showing signs of woodpecker predation were also similar on both plots (9 of 79 trees [11.4%] vs 7 of 41 trees [17.1%]). The following analyses are based on pooled data.

Based on dimensions of the excavations and on bird censuses of the clear-cuts (see below), we infer that Downy (*Picoides pubescens*) and Hairy (*P. villosus*) woodpeckers accounted for all of the excavations. Woodpeckers did not excavate borers randomly with respect to their orientation on tree trunks. Eleven of 22 borers excavated had entered trees from the

west side ($\chi^2 = 15.7$, df = 3, $P < 0.005$). Also, frequency of predation did not differ between trees with one and trees with more than one borer attack ($\chi^2 = 0.42$, df = 1, $P > 0.50$).

Both trunk diameter ($t = 2.17$, df = 232, $P = 0.031$) and height of borer attack site ($t = 2.02$, df = 232, $P = 0.044$) differed between excavated and nonexcavated borer chambers. Depredated borers were found in smaller trunks ($\bar{x} = 8.3$ vs 9.8 cm) and higher on trees ($\bar{x} = 186.5$ vs 149.4 cm) than nondepredated borers. Because height was significantly correlated with diameter ($r = -0.20$, $P = 0.002$), there may have been an interaction between these two variables, such that the true relationship between woodpecker predation and its controlling factor was obscured. To control for this potential bias, we used logistic regression analysis (PROC CATMOD, SAS Institute Inc. 1985) to determine the simultaneous effects of the continuous predictor variables (height and diameter) on the categorical response variables (depredated and nondepredated). Results of our analysis showed that trunk diameter ($P = 0.049$) was a better predictor of predation than was height ($P = 0.073$).

Discussion. —The 9.4% capture rate of borers in this study was low compared to mortality caused by woodpeckers in other studies. For example, Solomon (1969, 1975), summarizing data for more than a dozen species of wood borers, found that woodpeckers depredated 13 to 81% of the marked borers. As in our study, Solomon (1969, 1975) recorded predation of most species over one winter. In a study of red oak borers in southern Ohio, Hay (1972) credited woodpeckers with 39% of the total mortality over a two-year period, with nearly equal predation rates between the first (33%) and second (30%) overwintering periods.

The low predation rate in our study may have been due to the study plots being in clearcuts. Dense vegetation and lack of large trees make these areas less profitable foraging sites in comparison to surrounding woodlands (see Conner and Crawford 1974, Conner and Adkisson 1975, Conner 1980). In fact, we sighted only 10 Downy and 4 Hairy woodpeckers in 25 pairs of censuses (one in each plot) over a six-month period from October to April. Relative abundances of these same species were more than two times higher in the surrounding uncut forests (Petit et al. 1985).

Another potential explanation for the low predation rate was that we studied the red oak borers only during their second winter. The depths at which the borers were located within the trunks during the second winter (3–5 cm) were much different than during the first winter period (1–2 cm; see Donley and Acciavatti 1980). Thus, woodpeckers may be able to excavate borers more readily during the beetles' first winter, but more data are needed to confirm this idea.

We have no answer as to why most borer larvae that were depredated had entered tree trunks on the west side of the bole. Regardless of the side of the tree which a borer entered, woodpeckers could excavate the chamber from any side of the tree. We did not quantify the orientation of excavation sites, but there appeared to be no pattern as to the side selected. Tree diameter affected the probability of borer predation. Solomon (1969) found that woodpecker predation of red oak borers was limited to trees <15 cm in diameter. This relationship may be due to woodpeckers not being able to locate borers that are deeper within the boles of trees or to woodpeckers selecting small diameter trunks so as to reduce excavation time. Height of borer attack site also affected the chances of predation. Downy and Hairy woodpeckers may have selected those heights in which they were not vulnerable to ground predators and, yet, were not obstructed by the numerous branches higher on the tree trunk. This correlation, however, may have been affected to some extent by the interaction between diameter and height.

The low rate of borer mortality in this study suggests that, in regenerating hardwood clearcuts, woodpeckers may not be significant predators of borers overwintering deep within the boles of trees. This is not to say, however, that woodpeckers do not significantly reduce numbers of red oak borers during the first overwintering period (Hay 1972). The lack of

snags in clear-cuts may also be detrimental to populations of woodpeckers that may otherwise roost or nest there (e.g., Dickson et al. 1983; but see McPeek et al. 1987). This paucity of woodpeckers may, in turn, allow tree-damaging wood borers to remain relatively free of natural control provided by woodpeckers.

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