Factors Influencing Woodpecker Predation on Emerald Ash Borer

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ABSTRACT.—Woodpeckers are a significant source of mortality of emerald ash borer (EAB) (Agrilus planipennis Fairmaire), an Asian phloem-feeding insect first discovered in North America in 2002. However, factors that may influence woodpecker-EAB interactions have not been investigated. We collected data on woodpecker predation, EAB density and tree and site characteristics in southeastern Michigan, where EAB first became established. We tested statistical models to assess the ability of these variables to account for woodpecker predation levels. We observed foraging woodpeckers in the field to determine which species foraged on ash, and to compare the time spent foraging on ash vs. other tree species. Levels of woodpecker predation on EAB were variable, ranging from zero to 26.3 woodpecker attacks per m$^2$ for green ash (n = 15 sites) and from 2.3 to 37.1 attacks per m$^2$ for white ash (n = 7 sites). Woodpecker predation level was positively associated with the EAB density in a tree. White ash had higher predation levels than green ash, and less forested sites had higher predation levels than forested sites. However, these variables explained a relatively small amount of the variation in woodpecker predation level. Hairy, downy and red-bellied woodpeckers were observed foraging on ash trees. Woodpeckers spent significantly more time in foraging bouts on ash than on other tree species in EAB-infested areas. We suggest that managers of sites with substantial ash populations maintain conditions that are attractive to woodpeckers to encourage predation of EAB. Our analyses indicate that we need to understand much more about the foraging patterns of woodpeckers on EAB to be able to predict their impact on EAB populations.

INTRODUCTION

Emerald ash borer (EAB), Agrilus planipennis Fairmaire (Coleoptera: Buprestidae), threatens more than eight billion ash (Fraxinus sp.) trees in the continental U.S. EAB, native

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to Asia, was identified in 2002 as the source of widespread ash mortality in southeastern Michigan and Windsor, Ontario. Relatively little is known about EAB even in its native range, where it functions as a secondary pest of stressed, dying or recently killed ash (Yu, 1992; Cappaert et al., 2005a). All North American ash species that occur within the current EAB range have been killed by EAB, including white ash (*F. americana*), green ash (*F. pennsylvanica*), black ash (*F. nigra*), blue ash (*F. quadrangularis*) and pumpkin ash (*F. profunda*). This invasive pest has not coevolved with North American ash tree species and it is unlikely that native parasitoids or predatory insects will regulate EAB populations. To date, estimates suggest that more than 20 million ash trees have been killed by EAB in southeastern MI alone (Emerald ash borer, 2007).

Woodpeckers are the most important biotic source of mortality of EAB identified to date in the U.S. In some trees, woodpeckers have removed up to 95% of EAB larvae (Cappaert et al., 2005b), but our understanding of factors affecting woodpecker predation of EAB is limited. Here, we present exploratory analyses investigating factors that could potentially influence levels of woodpecker predation on EAB. Identification of such factors could improve the accuracy of models predicting the spread of EAB populations and suggest strategies that would enhance woodpecker predation on EAB.

Three woodpecker species in Michigan, the downy woodpecker, *Picoides pubescens*, the hairy woodpecker, *Picoides villosus*, and the red-bellied woodpecker, *Melanerpes carolinus*, are the most likely to forage extensively for EAB. All three are year-round residents in central and southern Michigan, where high EAB densities are common, and all use wooded habitats, ranging from mature forest to wooded residential areas (Brewer et al., 1991; Shackelford et al., 2000; Jackson and Oellet, 2002; Jackson et al., 2002). Low habitat suitability for woodpeckers has been suggested as a reason for low predation levels on wood-boring insects (Petit and Grubb, 1988). Thus, our first expectation was that sites with more forest cover would have more woodpecker predation than sites with less forest cover because forested sites provide better habitat for woodpeckers than open sites.

Numerous studies have demonstrated that woodpeckers, including the three species listed above, forage on pest species during outbreaks and sometimes respond both numerically and functionally, *i.e.*, changing their foraging behavior, when outbreaks occur (reviewed in Machmer and Steeger, 1995; Fayt et al., 2005). For example, Engelmann spruce beetles (*Dendroctonus obsesus*) made up a greater proportion of the stomach contents of hairy woodpeckers from heavily infested forests compared to birds from lightly infested forests (Koplin and Baldwin, 1970). Changes in prey availability may drive foraging site preferences as well. Downy and hairy woodpeckers foraged more commonly in trees infested with southern pine beetles (*D. frontalis*) than in uninfested trees in eastern Texas (Kroll and Fleet, 1979). Because ash trees that are heavily or lightly infested with EAB are often in close proximity to each other (Cappaert et al., 2005a), woodpeckers should be able to choose which trees to use relatively easily. Hence, our second expectation was that predation levels would be greater on heavily infested trees than on lightly infested trees.

Another potential influence on predation rates is the condition of the tree. Downy woodpeckers prefer foraging in dead trees or the dead portions of live trees, compared to the living portions of live trees (Conner et al., 1994). They often use dead trees for foraging, particularly in the winter months (Jackson, 1970). Hairy woodpeckers also show preferences for dead trees in some areas (Raphael and White, 1984; Morrison et al., 1987) and red-bellied woodpeckers commonly use dead limbs of live trees and snags (Williams, 1975; Conner et al., 1994). The rate at which trees succumb to EAB depends in part on the density of larvae, but also on tree vigor before and during the infestation. Trees in relatively good
TABLE 1.—Characteristics of study sites

<table>
<thead>
<tr>
<th>Name</th>
<th>Land-cover classification (Forest, Golf course/park/plantation or Urban/residential)</th>
<th>Percent forest within 250-m radius buffer</th>
</tr>
</thead>
<tbody>
<tr>
<td>AAC</td>
<td>Forest</td>
<td>26.7</td>
</tr>
<tr>
<td>AA East</td>
<td>Golf course/park/plantation</td>
<td>15.5</td>
</tr>
<tr>
<td>AA Saline</td>
<td>Urban/residential</td>
<td>7.7</td>
</tr>
<tr>
<td>AA West</td>
<td>Golf course/park/plantation</td>
<td>1.1</td>
</tr>
<tr>
<td>AH</td>
<td>Forest</td>
<td>18.2</td>
</tr>
<tr>
<td>A Jet D-1</td>
<td>Urban/residential</td>
<td>22.2</td>
</tr>
<tr>
<td>A Jet D-2</td>
<td>Urban/residential</td>
<td>24.8</td>
</tr>
<tr>
<td>Canoe</td>
<td>Forest</td>
<td>55.2</td>
</tr>
<tr>
<td>CH</td>
<td>Forest</td>
<td>71.4</td>
</tr>
<tr>
<td>Dart</td>
<td>Urban/residential</td>
<td>42.8</td>
</tr>
<tr>
<td>FF</td>
<td>Forest</td>
<td>30.9</td>
</tr>
<tr>
<td>For</td>
<td>Urban/residential</td>
<td>40.8</td>
</tr>
<tr>
<td>HH</td>
<td>Golf course/park/plantation</td>
<td>22.7</td>
</tr>
<tr>
<td>HM</td>
<td>Forest</td>
<td>29.1</td>
</tr>
<tr>
<td>KGC</td>
<td>Golf course/park/plantation</td>
<td>9.9</td>
</tr>
<tr>
<td>K-L</td>
<td>Forest</td>
<td>58.5</td>
</tr>
<tr>
<td>Lans</td>
<td>Golf course/park/plantation</td>
<td>20.4</td>
</tr>
<tr>
<td>Livonia</td>
<td>Urban/residential</td>
<td>18.8</td>
</tr>
<tr>
<td>M-52</td>
<td>Urban/residential</td>
<td>0.8</td>
</tr>
<tr>
<td>Maybury</td>
<td>Forest</td>
<td>71.0</td>
</tr>
<tr>
<td>Northville</td>
<td>Urban/residential</td>
<td>14.7</td>
</tr>
<tr>
<td>Novi</td>
<td>Urban/residential</td>
<td>43.1</td>
</tr>
<tr>
<td>SJMH</td>
<td>Golf course/park/plantation</td>
<td>31.1</td>
</tr>
<tr>
<td>Tempo 04-1</td>
<td>Urban/residential</td>
<td>19.6</td>
</tr>
<tr>
<td>Tempo 04-2</td>
<td>Urban/residential</td>
<td>20.6</td>
</tr>
<tr>
<td>Tempo 04-3</td>
<td>Urban/residential</td>
<td>25.9</td>
</tr>
<tr>
<td>Western</td>
<td>Golf course/park/plantation</td>
<td>16.0</td>
</tr>
</tbody>
</table>

condition, therefore, may be infested with EAB but less attractive to woodpeckers than those in poorer condition. Our third expectation was that trees in poor condition would have greater predation levels than trees in better condition.

We also examined the potential influence of two other variables, tree size and tree species, on the level of woodpecker predation. Downy, hairy and red-bellied woodpeckers all exhibit flexible foraging patterns, using a wide range of tree sizes (Shackelford et al., 2000; Jackson and Oellet, 2002; Jackson et al., 2002). It is possible that tree size may influence woodpecker use but we did not make a specific prediction regarding the direction of this effect. Also, tree species sometimes vary in their attractiveness to woodpeckers because of differences in chemistry or bark texture (Jackson, 1979). White ash and green ash, the two most common species encountered by EAB to date, may differ in the degree to which they are used by woodpeckers. Hence, we also tested tree species as a potential explanatory variable for the level of woodpecker predation.

METHODS

Site and tree selection.—Data from 27 sites in southeastern Michigan known to be infested with EAB were used for our analyses (Table 1, Fig. 1). These sites were initially used for studies examining pesticide efficacy or aspects of EAB biology. Sites used for pesticide
studies were located in landscape settings (mown park land or city streets) with high-value ash trees. Within sites, individual study trees were chosen to minimize variation between trees in condition, size and location. Only data from trees used as untreated controls in the pesticide trials were included in the analyses presented here. Sites for biology studies were located in unmaintained parklands and forests; these sites, and individual trees within sites, were chosen to represent diverse settings (open and closed canopy), EAB densities and tree size and species (white and green ash, *Fraxinus americana* and *F. pennsylvanica*). Data from the 27 sites, classified as: (1) forest, (2) open (golf course/park/plantation) or (3) residential/urban, were combined for the analyses.

Calculation of EAB density and woodpecker predation levels.—All trees from a site were sampled within a few weeks of each other except at two sites where the sampling occurred over several months. EAB sampling occurred from 2002 through 2005. The diameter at breast height (DBH), measured 1.3 m aboveground, and the species were recorded for each tree from which samples were taken. We visually estimated canopy dieback for each tree, which we used as an index of tree condition (Anulewicz, 2006). EAB density and woodpecker predation levels were quantified for 300–600 cm² "windows" cut through the bark on five to ten areas per tree. For each sampled area, the number of distinctive D-shaped exit holes left by emerging adult EAB and all woodpecker holes situated over the terminus of EAB galleries were recorded per unit area. Only woodpecker holes approximately the diameter of a woodpecker's bill were counted. Larger excavations, not clearly associated with the terminus of EAB galleries, were not included in these counts. It was not possible to determine with
confidence when holes were created. Thus, we did not attempt to distinguish the ages of the holes. Hereafter we refer to these woodpecker holes as attacks. The number of exit holes per m$^2$ was averaged on a per tree basis, as was the number of woodpecker attacks per m$^2$, to arrive at one EAB density and one woodpecker predation level per tree. The EAB density is an index of the relative level of resources (EAB larvae) that were available to woodpeckers in that tree. Our index of woodpecker predation, the number of woodpecker attacks per unit area of a sampled tree, describes the relative level of woodpecker activity on a tree that likely resulted in EAB mortality. Dissections of infested ash trees have shown that nearly every woodpecker attack occurs in winter or spring and results in mortality of an *Agrilus planipennis* prepupal larva. Prepupal larvae have completed their feeding and have a high probability of successfully emerging as adults in summer (McCullough and Siegert, in review). Thus, although our index of woodpecker predation does not describe the percentage of EAB larvae removed from a tree, it closely describes the number of potential EAB adults (larvae) that have been removed from a tree and the local EAB population.

We are confident that the predation we recorded represents woodpeckers feeding on EAB. Ash trees that are severely stressed, dying or are recently dead or cut, can be colonized by a handful of native wood-borers and bark beetles. On a few occasions, we have observed lilac borers (Lepidoptera), red-banded ash borer (Cerambycidae) and ash bark beetles (Scolytidae) on ash trees infested by EAB. These insects, however, were rarely recovered from any of the trees used for this study. Moreover, as forest entomologists (DGM and DC), we can readily distinguish EAB galleries and exit holes and those of other insects.

**Land-cover analyses.**—To calculate the proportion of forest cover surrounding sites with sampled trees, we obtained the IFMAP/GAP (Integrated Forest Monitoring, Assessment and Prescription System/Gap Analysis Program) Lower Peninsula Land Cover (2001) from the Michigan Department of Natural Resources. Land-cover data were generated from Landsat satellite imagery and classified into six major levels: urban, agricultural, bare/sparingly vegetated, upland open land, upland forest, water and wetlands. Data were further divided into 35 classes. We edited and manipulated the land cover, originally in the ERDAS Imagine image format, using ArcGIS 8.3 (2002). Coordinate locations of the center points of the study sites were plotted on the land cover. A 250-m radius buffer was applied to each center point, equaling an area of approximately 19 ha. Home ranges for downy woodpeckers range from approximately 2–12 ha (Jackson and Ouellet, 2002), whereas those for red-bellied woodpeckers range from less than 2 to 19 ha (Shackelford *et al.*, 2000). Data are lacking for hairy woodpeckers regarding home range. Hence, our 250-m buffers encompassed areas that would likely be used by several individuals of at least two of the woodpecker species. Also, the 250-m buffer was small enough that buffers from adjacent sites did not overlap. For eachbuffered site, we calculated the area and percentage covered by each of the 35 land classes. We then classified each of the 35 land classes as forest or non-forest. Forest included the following classes: aspen association, lowland coniferous forest, lowland deciduous forest, lowland mixed forest, mixed upland deciduous, northern hardwood association, oak association, other upland conifers, other upland deciduous, pines and upland mixed forest. We calculated the total area of these 11 forested classes, as well as the total area of non-forest classes, to determine the percent forested area in each buffer.

**Foraging observations.**—To determine which woodpecker species prey on EAB, and whether time spent foraging on ash and non-ash trees differed, we conducted observations of foraging woodpeckers at two sites where EAB is well-established: Hudson Mills Metropark, Dexter, MI, and Island Lake Recreation Area, Brighton, MI. On 9 d between Jan. and Apr.
2006, we walked through the areas between approximately 8:30 a.m. and 11:30 am. When a woodpecker was sighted on a live or dead tree, we immediately began recording the types of behaviors it engaged in and the duration of the behaviors. We continued recording until the bird left the tree. We considered the period of time one bird was observed on a tree as one observation. We did not conduct observations of more than one male and female of a species on the same day to avoid resampling individuals within a day. We tallied the duration of time spent in all behaviors associated with foraging including pecking, scaling, excavating, and peering and poking (Kilham, 1965) for each observation. We also consulted Remsen and Robinson (1990) on the behaviors woodpeckers exhibit while foraging.

Statistical analyses.—We used a G-test of independence with William’s correction to compare the proportions of white ash and green ash trees that had evidence of woodpecker predation. We used a Wilcoxon two-sample test to compare the mean number of woodpecker attacks on white ash and green ash.

We examined 31 potential models to explain the variation in woodpecker predation levels on individual ash trees. The potential models included all possible combinations, i.e., the one 5-variable model, all 4-variable models, all 3-variable models, etc., of the following explanatory variables: (1) proportion forest cover in the 250-m buffer surrounding each study site, (2) site type (forest, open [golf course/park/plantation] or urban/residential), (3) EAB density, (4) tree DBH and (5) tree species. The first two variables describe the amount of forest cover within and surrounding each site. Preliminary analyses showed that tree condition was highly correlated with the EAB density ($r = 0.48$, $P < 0.0001$, $n = 113$, Spearman correlation) so we excluded tree condition as a possible explanatory variable because condition is likely a consequence of the infestation level. None of the other continuous variables were significantly correlated with each other. The categorical variable site type was assessed in the regression equation with two dummy variables. For all potential models that included the variable site type, we included both dummy variables. We considered the first two variables above to be site-level variables and the other three variables to be individual tree-level variables.

Akaike’s Information Criterion (AIC) values for each model were calculated from least squares multiple regression models (SAS, version 9.1.3, 2006) following Burnham and Anderson (2002). These values were corrected because the ratio of sample size to the number of estimated parameters was less than 40 in all cases and hence are AICc values (Anderson and Burnham, 2002; Burnham and Anderson, 2002). The final model was chosen based on differences between competing models in AICc values and Akaike weights (Burnham and Anderson, 2002) and had the lowest AICc of all the models tested. We examined the residual plot for the final model to check that the model met the assumptions of linear regression. There appeared to be increasing variance in the residual plot, so we log-transformed the response variable, number of woodpecker attacks per m$^2$. The residual plot for the model with the log-transformed variable showed no increasing variance.

We compared the time spent on foraging behaviors when woodpeckers were observed on ash trees vs. non-ash trees with Wilcoxon two-sample tests. Woodpeckers that were observed on trees but did not engage in any foraging behaviors were excluded from these analyses. Statistical tests were carried out according to Sokal and Rohlf (1995) using SAS version 9.1.3 (2006).

Results

The dataset comprised 67 white ash trees and 97 green ash trees. Woodpecker predation was apparent on 114 of the 164 study trees (69.5%). Trees with and without woodpecker predation did not differ in dbh ($C = 4228.5$, $P = 0.71$), EAB density ($C = 4168.5$, $P = 0.88$),
Table 2.—Means (±SE), and ranges of woodpecker predation and potential explanatory variables of woodpecker predation levels on ash trees in southeastern Michigan

<table>
<thead>
<tr>
<th>No. of woodpecker attacks per m²</th>
<th>Proportion of forest cover around sampling sites</th>
<th>Site type*</th>
<th>EAB exit holes per m²</th>
<th>DBH (cm)</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>13.1 ± 20.9</td>
<td>28.1 ± 18.8%</td>
<td>type 1 = 56</td>
<td>22.2 ± 28.5</td>
<td>22.0 ± 12.9</td>
<td>white ash = 67</td>
</tr>
<tr>
<td>0–118.1</td>
<td>0.8–71.4</td>
<td>type 2 = 46</td>
<td>0.0–155.6</td>
<td>5.0–61.0</td>
<td>green ash = 97</td>
</tr>
<tr>
<td>n = 164</td>
<td>n = 27</td>
<td>n = 164</td>
<td>n = 164</td>
<td>n = 164</td>
<td></td>
</tr>
</tbody>
</table>

* Site type = 1 (forest), 2 (open), or 3 (residential/urban)

or the proportion of forest at sampling sites (C = 4001.5, P = 0.66). A significantly higher proportion of white ash trees showed woodpecker predation (79.1%) compared to green ash trees (62.9%, G = 5.01, df = 1, n = 164, P < 0.025). Woodpecker attacks per m² ranged from 0 to 118.1 for white ash (n = 67 trees) and from 0 to 56.7 for green ash (n = 97).

White ash trees had a higher mean number of woodpecker attacks per m² than green ash trees (18.1 ± 26.7 and 9.6 ± 14.9, respectively, Z = 2.51, n = 164, P = 0.01). On a site level, the mean number of woodpecker attacks per m² was extremely variable, ranging from 2.3 to 37.1 attacks per m² for white ash (n = 7 sites) and from 0 to 26.3 woodpecker attacks per m² for green ash (n = 15 sites). Only sites with at least three sampled trees were included in these calculations.

The means and ranges of the potential explanatory variables for predation levels on ash are in Table 2. The model with the predictor variables EAB density, tree species, and proportion of forest had the most support. This model explained 15.6% of the variation in the woodpecker attacks per m² (Table 3). Despite the result reported in the previous paragraph that trees with and without woodpecker predation did not differ in EAB density, trees with higher EAB density had more woodpecker attacks per m² (Table 3), according to the regression analysis. This is apparently a result of a positive correlation between the number of woodpecker attacks per m² and EAB density, for those trees with woodpecker predation (r = 0.45, P < 0.0001, n = 114, Spearman correlation). White ash had more woodpecker attacks than green ash and areas with less forest cover had more woodpecker attacks per m². The amounts of variation in woodpecker predation level explained by EAB density, tree species, and proportion of forest were relatively small (Table 3).

We observed woodpeckers foraging on ash trees ten times; observations included two downy woodpeckers, seven hairy woodpeckers, and one red-bellied woodpecker.

The mean time woodpeckers on ash trees engaged in foraging behaviors was 187.0 ± 161.9 s (n = 9) while the mean time on non-ash trees (n = 17) was significantly less (38.2 ±

Table 3.—Final regression model to explain woodpecker predation on white ash

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Explanatory variables</th>
<th>Parameter estimate ± (SE) (P-value)</th>
<th>df</th>
<th>Partial R²</th>
<th>Model-adjusted R² (P-value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of woodpecker attacks per m²</td>
<td>EAB exit holes per m²</td>
<td>0.25 ± 0.007 ± 0.002 (P &lt; 0.0001)</td>
<td>163</td>
<td>0.091</td>
<td></td>
</tr>
<tr>
<td>Species (white ash vs. green ash)</td>
<td>Species</td>
<td>0.467 ± 0.119 (P &lt; 0.0001)</td>
<td>0.057</td>
<td>0.156 (P &lt; 0.0001)</td>
<td></td>
</tr>
<tr>
<td>Proportion of forest</td>
<td>Proportion of forest</td>
<td>-0.006 ± 0.003 (P = 0.03)</td>
<td>0.024</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* W is the generalized Akaike weight, a measure of the level of evidence for a model
42.5 s, Wilcoxon two-sample test, C = 128.5, P < 0.005). The pattern was the same when we included only data from hairy woodpeckers foraging on ash trees (n = 6) and non-ash trees (n = 5). Hairy woodpeckers spent more time engaged in foraging behaviors when on ash trees (252.8 ± 159.7 s) compared to non-ash trees (43 ± 21.7 s, Wilcoxon two-sample test, C = 27, P = 0.025).

Mean daily temperatures were above average for southeastern Michigan during the winter/spring of 2006, when we made our observations. Total precipitation levels for the area were normal to slightly above normal for this same time period (Midwestern Regional Climate Center, 2006).

**DISCUSSION**

Despite the fact that all the explanatory variables in the final model had significant effects on woodpecker predation level, the effects were small (Table 3). Site-level variables such as proportion forest cover are unlikely to explain much of the variation in predation levels because predation levels on trees varied greatly within a site. Many sites had trees with 100% predation alongside trees with 0% predation. Thus, it was somewhat surprising that the site-level variable proportion of forest cover did have a significant, if small, effect. Tree species and EAB infestation levels, which are individual tree variables rather than site-level variables, also had significant, although minor, effects on predation levels. Apparently we are missing other important factors that influence predation on EAB.

Woodpecker predation levels on EAB will likely be affected by a number of variables including the age structure of ash trees and species composition of the entire tree assemblage within an area, the abundance of all food types, time of year, and the caloric value of the food (Fayt et al., 2005). Investigation of these variables, along with more detailed documentation of woodpecker foraging behavior, would help to clarify the relationships between site-level variables, tree-level variables, and woodpecker predation levels. For example, sites with conditions more favorable to woodpecker reproduction and juvenile dispersal, e.g., with appropriate nesting trees, are more likely to have woodpecker populations capable of playing a role in the maintenance of a pest species at an endemic rather than an epidemic level (Fayt et al., 2005). However, woodpecker density alone will not determine whether an individual tree is attacked because variables such as the species and condition of the tree, as well as the species and condition of neighboring trees, will influence whether a tree is selected for foraging. The relationship between woodpeckers and EAB is undoubtedly complex but deserving of further study, given the high likelihood of serious damage to ash populations throughout North America.

Our results showing that the time spent by woodpeckers foraging on ash was approximately five times greater than on non-ash indicate that woodpeckers are taking advantage of the food resource offered by EAB and may be helping to slow the spread of EAB by eating large numbers of the larvae. As a point of reference, trees with more than 60 exit holes per m² are considered to be heavily infested (Anulewicz, 2006; McCullough and Siegert, in press). In the trees we sampled, 16 (about 10%) had more than 40 woodpecker attacks per m² but most of these trees had less than 60 exit holes per m². This indicates that woodpecker predation was keeping the EAB density in these trees at low to moderate levels.

**Management recommendations.**—Landscape trees and high-value trees on a golf course or in a park that are infested with EAB can be treated with insecticides or replaced by alternative species. Unfortunately, however, managers of forested land have few silvicultural options in stands with a sizeable ash component. Silvicultural recommendations are difficult to develop because of the variety of sites that can be occupied by ash species. Moreover, ash occur at
varying levels with a wide range of other species. White ash, for example, is a common associate in at least 26 different forest cover types (Schlesinger, 1990; MacFarlane and Meyer, 2005). Guidelines for EAB management typically suggest that forest managers consider their specific site conditions, the EAB situation in their area, and their management objectives. Potential actions range from reducing ash basal area (e.g., by directed harvest or selecting against ash in Timber Stand Improvement (TSI) activities), encouraging regeneration of alternative species (via TSI, seeding, planting) or simply doing nothing and allowing the EAB infestation to run its course (e.g., Cook and McCulloch, 2007; McCullough, 2007). Based on the present work, we suggest that property owners and land managers strive to maintain environments that are attractive to woodpeckers, particularly hairy woodpeckers. For example, hairy woodpeckers typically use large living trees with internal fungal damage for nesting (Jackson et al., 2002) so maintenance of these types of trees in an area will provide appropriate nest sites. In areas where it would not pose safety issues, it would also be useful to avoid removing snags (standing dead trees) and dead branches on live trees because these types of sites are used by woodpeckers for foraging (Jackson, 1970; Williams, 1975; Conner et al., 1994).

The present study identifies several other avenues of research that would increase our understanding of interactions between woodpeckers and EAB and help to formulate strategies that could potentially take advantage of woodpecker predation as a part of EAB containment efforts. Exclosure experiments are needed to determine mortality rates of EAB, particularly prepupal larvae, with and without woodpecker predation, and the contribution of woodpecker predation relative to other mortality factors. It would be useful to determine the percentage of woodpecker diets that are composed of EAB larvae (perhaps through analyses of fecal samples) across sites that vary in EAB density to determine whether woodpeckers increase the proportion of EAB in their diets in heavily infested sites. In addition, we should determine how the proportion of EAB taken varies among seasons. These data would indicate the upper limits to the numbers of EAB that would be taken out of a system by woodpeckers. In addition, monitoring woodpecker predation over time in newly infested sites would determine how long it takes woodpeckers to discover EAB. Finally, it would be useful to continue to observe woodpecker foraging behavior to assess the relative importance of the different woodpecker species in preying on EAB. These types of data would allow a more complete assessment of the factors that influence woodpecker-EAB interactions and the potential for woodpeckers to slow the spread of EAB.

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