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Native bark-foraging birds preferentially forage in infected ash (*Fraxinus* spp.) and prove effective predators of the invasive emerald ash borer (*Agrilus planipennis* Fairmaire)

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ABSTRACT

Inadvertently introduced into North America in the 1990s, the invasive emerald ash borer (EAB, *Agrilus planipennis*) has been spreading across the Great Lakes Region resulting in widespread ash tree (*Fraxinus* spp.) mortality. Native woodpeckers and other bark-foraging insectivores represent one of the few potential natural predators of EAB in the U.S. In this study, we combined observational and destructive tree harvesting approaches to assess bark-foraging bird predation on EAB larvae in a deciduous forest of central Ohio. Results of our observational study show that in an EAB impacted forest, bark-foraging birds forage more heavily on ash trees than non-ash trees, and that they forage preferentially on ash trees that exhibit canopy decline symptoms relative those with healthy canopies. These patterns were further supported by the destructive sampling of 46 ash trees wherein predation by bark-foragers significantly reduced tree-level EAB densities by upwards of 85%. Bark-foraging predation intensity increased with increased EAB infestation levels, with bark-foragers harvesting ~45% of EAB in trees with thinning canopies compared to ~22% in ash trees with healthy canopies. Woodpeckers harvest EAB in a density-dependent pattern that could contribute to population control. Despite bark-forager predation, EAB had a high likelihood of successfully emerging from the heavily infested ash trees (~30% or 35 EAB per m^2). Our results suggest that woodpeckers and other bark-foragers may use visual canopy decline, and perhaps other cues, to target ash trees with increased EAB densities. Moreover, our results provide insight into the indirect effects of invasive species on biotic interactions in forest ecosystems highlighting potential shifts in bark-foraging and other bird behaviors in response to a novel forest pest. Bark-foragers respond to EAB infestation and may thus potentially help regulate EAB populations and their spread in a mixed deciduous forest. We suggest that maintaining snags and nesting sites during and after forest pest outbreaks may enhance populations of bark-foraging bird species and, thus, their biological control of pest insects in temperate deciduous forests.

1. Introduction

Global commerce transfers, accidentally or intentionally, non-native species between continents (Mack et al., 2000; Wells et al., 1986). When invasive, these introduced species often exert multiple ecological effects, including changes in plant community composition, ecosystem function, and biotic interactions among and between native species (Allen et al., 2006; D'Antonio and Vitousek, 1992). The emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), an invasive forest pest, has been spreading across North America since its introduction to southern Michigan in the 1990s (Haack et al., 2002; McCullough and Katovich, 2004; Pugh et al., 2011; Flower et al., 2013a). The EAB is a small, elongate tree boring beetle (larval length: 26–32 mm, adult length: 7.5–15 mm), native to northeastern China, Mongolia, Japan, Korea, Taiwan, and Russia (Bauer et al., 2003; Yu, 1992). In its native range, EAB is considered a secondary forest pest only attacking trees experiencing physiological stress or those in later stages of senescence. Yet in North America, EAB indiscriminately kills healthy trees as well. EAB seems to feed exclusively on

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ash trees, infesting all *Fraxinus* spp. thus far encountered (Poland, 2007; Rebek et al., 2008).

During the summer, EAB adults lay upwards of 90 eggs on the bark surface. Larvae burrow into and feed in the cambium layer (phloem) of mature trees, overwinter in prepupal chambers in the trunk, pupate and finally emerge the following summer. Under inclement conditions, development may take 2 years (Lyons et al., 2004; Cappaert et al., 2005). While foraging, EAB larvae create conspicuous serpentine galleries that can lead to chronic water stress of trees and canopy decline (Flower et al., 2011, 2013b).

Woodpeckers, along with nuthatches and brown creepers, as bark-foraging insectivores, could provide some relief for ash trees in North America particularly if they preferentially feed on and in areas with infected ash trees. Through numerical and functional responses, observational and experimental (exclosure) studies, in conjunction with simulation modeling, suggest that woodpecker predation can potentially regulate the population dynamics of pests such as bark beetles (Fayt et al., 2005; Knight, 1958). Woodpeckers do prey upon EAB (Cappaert et al., 2005; Duan et al., 2010; Lindell et al., 2008) and their predation rates have been previously correlated with EAB density (Lindell et al., 2008). Furthermore, some woodpecker species and the white-breasted nuthatch (*Sitta carolinensis*) have shown increased densities in EAB infested regions (Koenig et al., 2013).

Several studies have directly assessed the patch use strategy of woodpeckers and other bark-foragers (*e.g.*, Lima, 1984; Olsson et al., 1999; Whelan and Maina, 2005). This knowledge of foraging strategies can be used to link the behaviors of woodpeckers and other bark-foragers to their efficacy in pest management. Foragers use one of three primary patch use strategies (Brown and Morgan, 1995): (1) fixed search time, (2) fixed harvest quantity, and (3) fixed quitting harvest rate (Brown and Mitchell, 1989; Fig. 1). Under a fixed search time foraging strategy, a forager spends a set amount of time within each patch, after which it leaves. This strategy may be adaptive for a forager that cannot estimate the value of each food patch. Under a fixed quantity foraging strategy, a forager remains in a patch until it has consumed a fixed quantity of resources. This strategy permits a forager to meet its minimal energetic or nutritional requirement. Under a fixed quitting harvest rate strategy a forager harvests each patch until its gains no longer sufficiently cover its foraging costs (Brown, 1988). This strategy is optimal for foragers that can accurately assess patch quality. If the bark-foraging bird species use a quitting harvest rate foraging strategy, they will recognize and bias their feeding towards trees with high EAB densities. Such a strategy is most propitious for slowing the spread of a pest such as EAB.

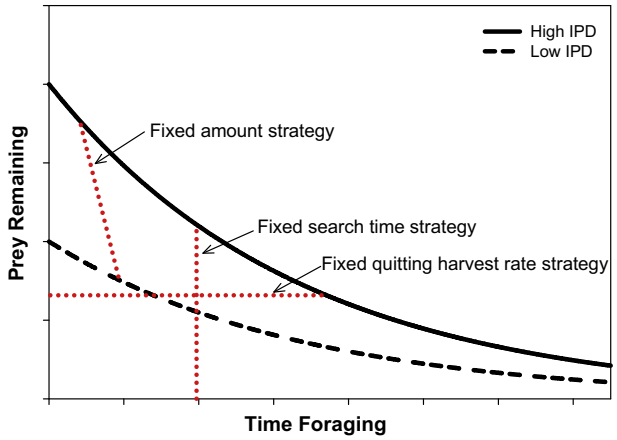

Fig. 1. Harvest model depicting the amount of prey remaining over time in high and low initial prey density (IPD) situations (solid and hashed lines respectively). Foraging strategies (fixed amount, fixed search time, and fixed quitting harvest rate) are denoted by dashed red lines. With a fixed amount strategy, proportionally less prey is consumed with greater IPD (note the quantity of prey harvested is comparable between high and low IPD); with a fixed search time strategy, about equal proportions of food are consumed regardless of IPD; with a fixed quitting harvest rate strategy, proportionally more food is consumed with greater IPD.

Here, we address two primary questions regarding the response of bark-foraging bird species to EAB infestation. First, what is the tree-level impact of bark-foraging birds on EAB within an infested forest stand? Previous studies (*e.g.*, Koenig et al., 2013) found a regional response of some bark-foraging species to EAB infestation, but little is known about within-stand responses. Second, we assess the patch use strategy of woodpeckers and other bark-foraging birds on EAB infested trees. Do these bird species use a strategy that might contribute to the control of EAB?

2. Methods

2.1. Study site

The study was conducted in a ~15 ha early-mid successional deciduous woodland located at Dempsey Middle School in Delaware, Ohio from 2008 to 2009. The dominant trees were white ash (*Fraxinus americana*), green ash (*F. pennsylvanica*), black cherry (*Prunus serotina*), red maple (*Acer rubrum*), elm (*Ulmus* sp.), and black walnut (*Juglans nigra*); understory species included boxelder (*Acer negundo*), honeysuckle (*Lonicera* spp.), and saplings of the canopy species. Ash trees at the site were infested with EAB as early as 2005, following the accidental importation of infested wood to an adjacent woodlot, and as determined by the appearance of D-shaped exit holes in 2006 (Knight et al., 2010).

2.2. Bark foraging guild

The bark-foraging birds in Ohio's forests include seven species of woodpecker (red-headed, *Melanerpes erythrocephalus*; red-bellied, *Melanerpes carolinus*; northern flicker, *Colaptes auratus*; yellow-bellied sapsucker, *Sphyrapicus varius*; downy, *Picoides pubescens*; hairy, *Picoides villosus*; and pileated, *Dryocopus pileatus*), the white-breasted and red-breasted (*Sitta canadensis*) nuthatch, and brown creeper (*Certhia americana*). Because of their widespread abundance, downy, hairy, and red-bellied woodpeckers and the white-breasted nuthatch are likely the most important avian predators of EAB in Ohio and throughout the expanding range of the EAB. Each of these species forages for EAB (Lindell et al., 2008; L. Long unpublished data). Pileated woodpeckers would be capable of feeding on EAB larvae (Bull and Jackson, 2011), but low densities may preclude them from major importance. Red-headed woodpeckers feed largely by aerial hawking and ground pouncing in the summer (Smith et al., 2000), and on mast, seeds and grains during winter, and are thus not likely important consumers of EAB. Northern Flickers forage principally on the ground, though they occasionally excavate carpenter ants (Wiebe and Moore, 2008). Brown creepers likely do not consume EAB larvae because they typically glean prey from bark surfaces and furrows. Red-breasted nuthatches are present only in winter, and they may consume over-wintering EAB larvae.

2.3. Woodpecker observational data

Two 200 m transects were established within the forest. Each transect was arranged between two random points. Points were delineated so that a 50 m buffer existed between each transect and any edge-like habitat. This reduced biases in detection frequency caused by edge effects. Woodpecker presence and abundance data were collected by slowly walking along each transect and recording all bark-gleaning birds, either audibly or visually,

within 50 m of the observer. Observations were conducted twice in 2008 (July 18 and July 25).

In late August 2008 the DBH and presence or absence of woodpecker foraging holes was recorded on the stem of each ash and non-ash tree >10 cm DBH within three meters of either side of each transect. When necessary, binoculars were used to aid with foraging hole identification in the canopy. For each ash tree, we rated its canopy condition class (AC, see Section 2.5 for description of canopy condition classes) (Smith, 2006; Flower et al., 2013b). Finally, we counted woodpecker holes on each stem within a measured range at breast height (1.25–1.75 m from the ground). The presence or absence of woodpecker holes was carefully documented by visually examining each stem with binoculars. Total forest area inventoried along each transect in this manner was 1200 m^2.

We also utilized three 11.28 m radius plots spaced $\geqslant$50 m apart to assess woodpecker preference for ash vs. non-ash. In these plots, all trees >10 cm DBH were measured and if an ash tree, we rated its AC class. Again, we counted woodpecker holes on each stem and documented the presence or absence of woodpecker holes visually as described above. The total forest area inventoried in the plots was 1200 m^2.

2.4. Tree selection and processing

Following leaf expansion in 2008 and 2009, mature ash trees (see Table 1) were chosen using a stratified random sample procedure. Trees were stratified by AC class and randomized within AC. Additionally we measured the diameter at breast height (DBH, ~1.37 m from ground level). During the winter following each growing season (December 2008 and January 2010), trees were felled, limbs removed, and the main stem was cut into 1 m segments. Following this, holes in the bark of the main stem were counted and painted according to certain characteristics. EAB emergence holes (D-shaped exit holes) were painted red, distinct woodpecker holes were painted blue, and other insect holes were painted yellow. After all holes were painted, bark was manually removed from each stem segment using a draw-blade. Bark removal revealed the painted holes allowing us to determine the fate of each individual EAB larvae. We tallied the number of EAB larval galleries (gal.) that terminated in an EAB D-shaped exit hole, the number of EAB larval galleries that terminated in a woodpecker or bark-foraging bird holes (WP), and the number of live and dead EAB larvae that remained in the tree. Total EAB abundance (initial prey density, IPD) was determined by Eq. (1) below:

$$\text{Total EAB} = \text{Live larvae} + \text{Dead larvae} + \text{Gal. ending in WP} + \text{Gal. ending in exit} \quad (1)$$

The destructive tree harvest approach described above allows assessment of the long-term cumulative foraging of woodpeckers and other bark-foragers over a period of 3–4 years. This approach provides the opportunity to assess the foraging behavior of bark-foraging bird's towards EAB in ash trees across a heterogeneous landscape. Because this study was not conducted in a single season, potential temporal variability of woodpecker densities was minimized (Jackson, 1970).

2.5. Ash canopy condition classes

The ash tree canopy condition (AC) method was designed to rapidly identify tree-level EAB symptoms (adapted by Smith, 2006 from Ball and Simmons, 1980). Ash canopy condition has been shown to exhibit a significant relationship with tree-level EAB densities (larvae/adult) and EAB gallery cover and thus it represents a good visual proxy for EAB infestation levels (Flower et al., 2010, 2013b). AC is graded on a scale from 1 (healthy) to 5 (dead): (1) healthy/full canopy – a healthy ash canopy is full and exhibits no defoliation; (2) thinning canopy – slight reduction in leaf mass, all top branches exposed to sunlight have leaves; (3) dieback – canopy is thinning and some top branches exposed to sunlight are defoliated, lower branches which exhibit natural thinning are not considered; (4) >50% dieback – the canopy has less than 50% of the leaves of a class 1 tree and/or over half of the top branches are defoliated; and (5) dead canopy – no leaves remain in the canopy portion of the tree, regardless of epicormic sprouts (Smith, 2006).

2.6. Statistical analysis

We assessed the relationship between tree species (ash and non-ash) and woodpecker foraging (woodpecker present vs. absent) individually across both transects and plots using two-tailed Fisher's exact probability tests ($P < 0.05$). To test for differences in the density of woodpecker holes/m^2 within the 1.25–1.75 m focal area between ash trees of different canopy condition classes and non-ash trees we used a one way analysis of variance (ANOVA, $\alpha = 0.05$). Data was normalized prior to analysis using a log(number of WP holes + 1) transformation. Because of low sample sizes of AC 3 and AC 4 ash trees, data from plot and transect measurements were pooled and AC 3 and 4 combined. We used post hoc Tukey's HSD pairwise comparisons ($P < 0.05$) to test differences between ash trees with different canopy conditions and non-ash.

We used a multivariate analysis of variance (MANOVA) to analyze the effect of AC on the dependent variables of total EAB abundance, EAB consumed by woodpeckers and other bark-foraging birds, and EAB emergence. Ash canopy condition was treated as a categorical variable. Dependent variables were surface area corrected (tree surface area = sum of all segment surface areas; segment surface area = π(DBH) (segment height); permitting comparison between trees of different diameters and heights). Following surface area corrections, dependent variables were log(dependent variable + 1) transformed prior to analysis to meet assumptions of normality. Univariate *F*-tests revealed significance for each independent variable allowing further investigation of differences in AC classes using protected ANOVA followed by post hoc comparisons between ash canopy condition classes using Tukey's HSD ($\alpha = 0.05$).

Table 1
Summary characteristics of destructively harvested focal ash trees. AC denotes ash condition class and n is the number of trees in the ash condition class. Values represent descriptive statistics (means ± SE); superscripts denote significance between AC classes (only comparable within column) associated with univariate ANOVA's conducted on transformed data detected by post hoc Tukey's HSD.

AC	*n*	DBH (cm)	Surface area (m^2)	# of EAB (m^2)	EAB galleries ending in exit hole (m^2)	EAB galleries ending with bark-forager hole (m^2)
1	11	12.2 ± 3.7	1.89 ± 0.57	11.5 ± 3.4^{c}	0.6 ± 0.2^{c}	2.6 ± 0.7^{c}
2	12	13.9 ± 4.0	2.47 ± 0.78	32.8 ± 9.5^{b}	2.4 ± 0.7^{c}	10.1 ± 2.9^{b}
3	11	14.2 ± 4.3	2.47 ± 0.75	87.8 ± 26.5^{a}	10.0 ± 3.0^{b}	31.8 ± 9.6^{a}
4	12	14.8 ± 4.3	2.69 ± 0.78	116.8 ± 33.5^{a}	34.7 ± 10.0^{a}	52.3 ± 15.1^{a}

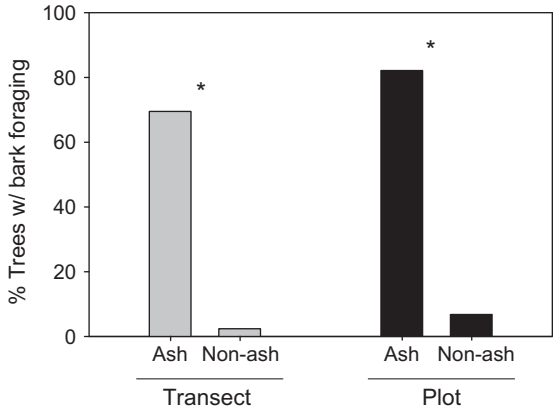

Fig. 2. The relationship between tree species (ash vs. non-ash) and evidence of attack by bark-foraging bird species from transect (grey bars) and plot (black bars) spatial scales. Asterisk denotes significance between ash vs. non-ash for the transect method ($P < 0.001$) and between ash vs. non-ash associated with the plot method ($P < 0.001$).

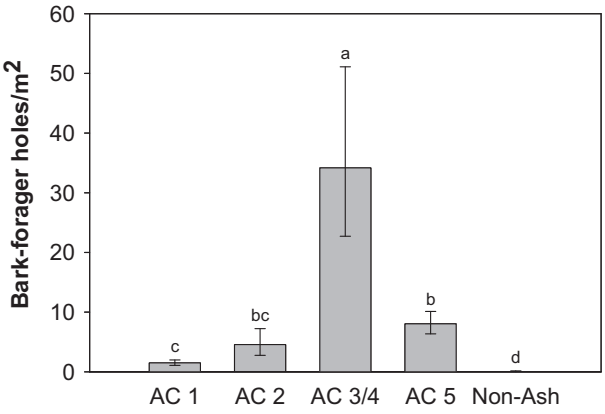

Fig. 3. Density of holes/m^2 of bark-foraging bird species across ash trees (AC 1–AC 5) and non-ash trees pooled from transect and plot measurements. Values represent back transformed means (±SE), superscripts denote significance levels ($P < 0.05$) associated with post hoc Tukey's HSD.

We used an analysis of covariance (ANCOVA, $\alpha = 0.05$) to analyze the effect of ash condition class on the dependent variable of the cumulative giving up density (GUD; the number of EAB remaining in the tree), with the initial prey density as a covariate. The cumulative GUD was log transformed prior to analysis to meet assumptions of normality. We also used an ANCOVA to analyze the effect of ash condition class on the dependent variable of proportion harvested, with the initial prey density (adjusted for EAB that had emerged) as a covariate. Initial prey density was normalized using a $\log(x + 1)$ transformation prior to analysis. In both analyses ash canopy condition class was treated as a categorical variable. Three trees were removed from analysis because they exhibited no evidence of EAB and thus did not constitute a foraging patch with EAB; a fourth tree was removed (only from the second analysis) because it exhibited only EAB emergence holes. Fisher's exact probability tests were conducted using VassarStats (www.vassarstats.net; Lowry, 2000), while the MANOVA and ANCOVA tests were conducted using SYSTAT version 12.

3. Results

3.1. Woodpecker observations

Woodpecker foraging (*e.g.*, presence of woodpecker holes) was more prevalent on ash trees relative to non-ash trees and these results were consistent when using both transect and plot based approaches (Fig. 2; Fisher's exact probability tests; transect $P < 0.001$, $n = 23$ ash and 83 non-ash; and plot $P < 0.001$; $n = 28$ ash and 44 non-ash). When looking at the 1.25–1.75 m stem portions of ash and non-ash trees along the two 200 m transects and in the plots, we found significant differences between tree species and ash canopy condition classes (ANOVA $F_{4,175} = 43.147$; $P < 0.001$; Fig. 3). On average ash trees had more woodpecker holes (21.10 ± 5.33 holes/m^2) relative to non-ash trees (0.29 ± 0.17 holes/m^2) (Fig. 3). Within the ash trees, trees with healthy canopies had significantly lower densities of woodpecker holes relative to trees exhibiting canopy decline (Fig. 3). During our bird observations, we observed three species of woodpeckers: downy, hairy and red-bellied woodpeckers.

3.2. Destructive tree harvesting

We counted evidence for 7098 EAB larvae in 46 different sample trees, of which 2624 had been harvested by woodpeckers and other bark-foraging birds, representing a predation rate of ~37% (range 0–85%). The density of EAB larvae/m^2 exhibited a significant positive relationship with ash tree canopy condition (MANOVA; $F_{3,42} = 23.491$; $P < 0.001$), indicating that increased EAB larval density may be responsible for the decline in trees canopy condition (Table 1). Similarly, EAB emergence was significantly related to AC (MANOVA; $F_{3,42} = 35.790$; $P < 0.001$). Woodpeckers and other bark-foraging birds harvest more EAB from ash trees experiencing canopy decline relative to trees with healthy canopies (MANOVA; $F_{3,42} = 24.382$; $P < 0.001$). Relatively speaking, the proportion of EAB emerging and the proportion of EAB larvae consumed by woodpeckers and other bark-foraging birds increased as tree canopy health declined, while the proportion of larvae remaining decreased (Fig. 4). This pattern of increased predation of EAB larvae associated with increased prey density is consistent with a quitting harvest rate foraging strategy (Fig. 1). Further analysis revealed that bark-foraging birds' giving up density of EAB was not related to the tree's canopy condition (ANCOVA; $F_{3,38} = 1.68$; $P = 0.194$) but instead varied according to the initial prey density (ANCOVA; $F_{1,38} = 297.6$; $P < 0.001$). Specifically, ash tree's containing higher initial prey densities of EAB exhibited higher GUD's. A higher

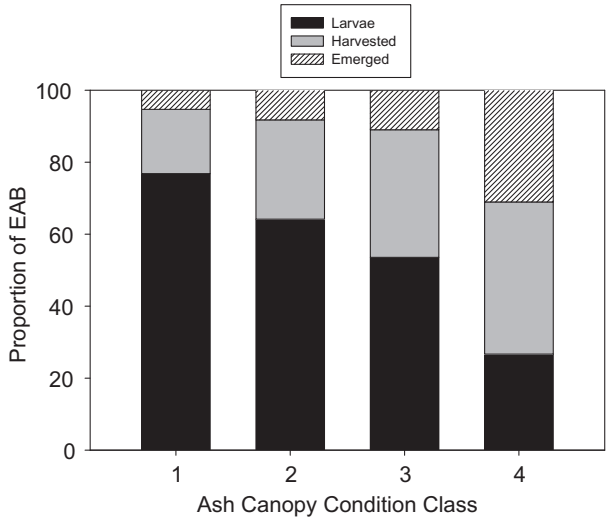

Fig. 4. Fate diagram depicting the proportion of EAB that emerged, were consumed by bark-foraging bird species (harvested), and remain living (larvae) across ash canopy condition classes.

proportion of EAB were harvested from trees with declining canopies relative to healthy canopies (ANCOVA; $F_{3,37} = 4.417$; $P = 0.009$), while initial prey density did not covary with the proportion of EAB harvested ($F_{1,37} = 1.458$; $P = .235$; Fig. 4). This is consistent with a fixed quitting harvest rate strategy where the woodpeckers gain information on the patch's value through sampling and harvest (e.g., Bayesian foraging, Olsson and Brown, 2006).

4. Discussion

In this study we examined within stand responses of birds in the bark-foraging guild to EAB invasion and found that members of this guild not only preyed on EAB, but shifted their foraging efforts toward ash trees (Fig. 2). Additionally, birds in the bark-foraging guild concentrated their foraging efforts on highly EAB impacted trees (Fig. 3). The bark-foraging guild's shift towards ash trees is not surprising and is consistent with previous observations that avian insectivores, including woodpeckers, often respond rapidly to forest pest outbreaks (Kilham, 1965; Fayt et al., 2005; Barber et al., 2008; Drever et al., 2009) or disturbances that increase the abundance of standing dead trees (Covert-Bratland et al., 2006). While impossible to ascertain if any of the bark foragers in our forest preferred to forage on ash relative to other species before the EAB outbreak, other studies have indicated either no preference towards ash in mixed deciduous forests (Jackson, 1970; Reller, 1972) or increased ash preference of male downy woodpeckers in low wind situations (<2 m/s^{-1}), but not female downy woodpeckers, black capped chickadees, tufted titmouse, or white breasted nuthatch (Grubb, 1975). A study by Willson (1970) indicated preferential utilization of ash trees by the white-breasted nuthatch and female red-bellied woodpecker, but neither over- nor under-utilization by brown creeper, red-headed, male red-bellied, or downy woodpeckers.

Below we discuss the evidence revealing the patch use strategy of bark-foraging birds in a central Ohio forest stand. We then consider the consequences for the community of potential EAB bark-foragers in this stand and the dynamics and further spread of EAB. Finally, we discuss implications of the response of the bark-foragers to EAB from the perspective of other tree species and other forest pests.

A particular strength of this study was the destructive harvesting of trees, which allowed us to fully account for the fate of all EAB larvae infesting a focal tree. Unlike window sampling which has been previously deployed, this sampling technique revealed that the giving up density on EAB larvae by bark-foraging birds increased with increasing infestation levels of EAB. This pattern of consumption is consistent with woodpeckers and other bark-foraging birds using an informed fixed quitting harvest rate approach, or more specifically, a Bayesian strategy (Figs. 1 and 4; Brown and Mitchell, 1989; Olsson and Holmgren, 1999; Olsson and Brown, 2006). With a Bayesian patch use strategy, foragers estimate patch quality using information about number of prey harvested from a patch, patch search time, and prior knowledge of patch quality distribution (Green, 1980; Iwasa et al., 1981; Olsson et al., 1999; Olsson and Brown, 2006).

While the mechanism bark-foraging birds use to detect and recognize infestation levels of boring beetles like EAB is unknown, at least two alternatives (not necessarily mutually exclusive) seem plausible. First, birds may simply use trial and error pecking, concentrating foraging efforts on trees with greater success rates. Second, birds may learn to recognize the differences in tree canopy health that humans recognize and use to characterize ash canopy classes. Specifically, as ash trees become impacted by EAB, individual leaf area is reduced (Flower et al., 2011) and their canopies thin as they drop leaf tissue (Smith, 2006; Flower et al., 2013b). As the tree-level infestation becomes more severe, bark begins to split and sloughs off, although this typically follows tree mortality and none of the destructively harvested trees were dead or exhibited noteworthy bark splitting.

Our data suggest that bark-foraging birds in this stand responded to increased infestation by EAB. With increasing infestation, and hence, greater canopy decline, we found increased numbers of EAB harvested, and an increased proportions of EAB harvested (Table 1, and Fig. 4). Many studies have shown that birds respond to herbivore telltale cues, including visual signals such as foliage damage (Heinrich and Collins, 1983), spectral reflectance of leaves (Mäntylä et al., 2007), and even emissions of volatile organic compounds (Mäntylä et al., 2008). Although we observed increased numbers of EAB larvae eaten by woodpeckers in trees with progressive canopy decline (AC 3 and 4) relative to healthy canopy conditions (AC 1 and 2), the bark-foraging birds at our site appeared to use the initial prey density rather than the progressive canopy decline that accompanies EAB infestation to inform foraging.

Optimal patch use as described by Brown (1988) indicates that foragers allocate their foraging efforts to patches in the environment that yield higher harvest rates than the environment at large. Hence, bark-foragers may perceive trees in AC 3 and 4 as rich patches that support high net energy intake, and thus concentrate their foraging efforts in those individual trees. By adopting a Bayesian foraging strategy, bark-foraging birds react to and potentially have a substantial impact on EAB population densities. A Bayesian strategy results in a "controlling" functional response (Mitchell and Brown, 1990; Olsson and Holmgren, 1999; Olsson and Brown, 2006) where a larvae's chance of being preyed upon increases with the number of larvae on the tree.

As pointed out by Cappaert et al. (2005) and Lindell et al. (2008), the invasion of EAB in North America spells doom for the various ash species but a boon for woodpeckers, and we would add, nuthatches. Koenig et al. (2013) examined Breeding Bird Survey records with respect to the history of EAB invasion in Michigan and Ohio, and they found evidence for numerical responses most likely owing to enhanced survival and/or reproduction in response to the EAB invasion within the impacted areas. Our data, based on within-stand consumption of EAB by bark-foraging birds are consistent with these previous studies.

Bark-forager predation of EAB was prevalent, with 85% of the destructively harvested ash trees (39 of 46 trees, note in three trees EAB were absent) displaying evidence of bark-forager predation of EAB. With predation rates averaging ~37% and as high as 85% in some trees, bark-foragers may play a significant role in the control of EAB at the stand level. Similar rates of woodpecker predation have been observed on western pine beetle (*Dendroctonus brevicomis*), ~32% (Otvos, 1965), on EAB ~ 17% (Duan et al., 2010) to 44% (Cappaert et al., 2005), and upwards of ~70% in mountain pine beetle (*Dendroctonus ponderosae*) (Dahlsten and Stephen, 1974). Such predation rates and the use of a Bayesian foraging strategy may effectively slow the spread of EAB and other forest pests across the landscape by reducing population sizes, although this assertion needs confirmation. Ultimately, in the case of EAB outbreaks, which become more severe over time, the infested trees will succumb to mortality.

Although untested, the concentration of foraging of the bark-foraging birds in this stand on ash trees observed in this study may alter the dynamics between trees and insects within this forest. Because of the concentration of foraging on ash trees, particularly those with high infestation levels, other forest pest species that infest trees other than ash may obtain a degree of associational refuge from predation by bark-foraging birds (Atsatt and O'Dowd, 1976; Pfister and Hay, 1988). These forest pests may include the European elm bark beetle (*Scolytus multistriatus*), the

Asian longhorned beetle (*Anoplophora glabripennis*), the gypsy moth (*Lymantria dispar*), among others. Shared doom or short-term apparent competition, on the other hand, may occur if the numerical response of bark-forgers drawn into the forest patch because of EAB leads to overall increased consumption of bark-dwelling insects within the stand.

Future studies should investigate numerical and functional responses of woodpeckers and other bark-foraging birds to this and other invasive forest pests. One such study by Koenig et al. (2013) documented a numerical response of red-bellied woodpeckers and white-breasted nuthatches following EAB invasions around the infestation epicenter. Similarly, Rabenold et al. (1998) observed increased abundance of hairy woodpeckers following the outbreak of balsam wooly adelgid (*Adelges piceae*) in spruce-fir forests of the southern Appalachians. Koenig et al. (2011) also observed similar population responses in seven species of North American woodpeckers following gypsy moth (*Lymantria dispar*) outbreaks. Increased density and richness of bark-insectivores, but not other foraging guilds, was observed by Drever et al. (2009) in response to mountain pine beetle outbreaks in British Columbia, Canada. Many bark-foragers are winter residents, which may help explain these strong numerical responses to pulsed resources. Such responses may have lasting impacts on biotic interactions in forest systems beyond the duration of the pest disturbance. Alterations in the foraging ecology of bark-foraging insectivores in response to forest pest disturbances may have negative trickle down effects on other native bark boring insects which may be selectively targeted in response to this new behavioral strategy. Furthermore, additional observational studies investigating the behavioral responses of woodpeckers and other bark-foraging birds to forest pest disturbances should be undertaken to assess which species are responding to these outbreaks.

4.1. Forest management implications

Management of EAB impacted forests should carefully weigh the value of retaining snags vs. tree removal with management objectives. Birds utilize snags as a foraging substrate, nesting substrate, perching habitat in which to search for prey, and for territorial announcements (Conner, 1978). The availability of snags has been shown to affect the abundance, diversity and species richness of woodpeckers and other cavity-nesting birds (Raphael and White, 1984; Zarnowitz and Manuwal, 1985). Maintenance of snags in forest stands should be undertaken to ensure cavity-nesting bird habitat following disturbances. This can be done by retaining standing dead trees or by deploying nest-boxes if tree removal is required (Caine and Marion, 1991; McComb and Noble, 1981; Wiebe, 2011). Downy woodpeckers have been suggested to prefer forest stands with $\geqslant$5 snags > 15 cm dbh/0.4 ha (Schroeder, 1983). Dead ash trees have been shown to break-up and fall quickly, with over half of dead ash trees falling within 4 years of mortality (Knight, unpublished data). As EAB impacted trees decay and fall, managers may need to supplement forests experiencing abundant tree fall with nest boxes. Further studies should investigate whether selective foraging of EAB in response to outbreaks will lead to woodpecker and bark-foraging bird population responses. Such studies will provide invaluable information regarding demographic responses of bark-foraging insectivores to forest pest outbreaks. In particular, as EAB infestation is an ephemeral phenomenon that essentially ends with the loss of ash from infested forest stands; will increased numbers of bark-foragers at that time result in increased pest control services for other tree species within those stands? Forest management practices that enhance woodpecker and bark-foraging bird habitat (*e.g.* maintenance of snags for nest holes) may create more resilient forests via the pest reduction services provided by avian insectivores (Whelan et al., 2008).

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