



Temporal dynamics of woodpecker predation on emerald ash borer (*Agrilus planipennis*) in the northeastern U.S.A.

David E. Jennings*, Jian J. Duan†, Leah S. Bauer‡, Jonathan M. Schmude†, Miles T. Wetherington* and Paula M. Shrewsbury*

*Department of Entomology, University of Maryland, 4112 Plant Sciences Building, College Park, MD 20742, U.S.A., †Beneficial Insects Introduction Research Unit, USDA Agricultural Research Service, 501 South Chapel Street, Newark, DE 19711, U.S.A., and ‡Northern Research Station, USDA Forest Service, 3101 Technology Boulevard, Lansing, MI 48910, U.S.A.

- Abstract**
- 1 Woodpeckers (Picidae) are important natural enemies attacking emerald ash borer (EAB) *Agrilus planipennis* Fairmaire in North America. There can be considerable variation in predation levels within and between sites, and among different times of year; therefore, understanding what causes these differences is necessary for effectively predicting EAB population dynamics.
 - 2 We examined the temporal dynamics of woodpecker predation on EAB in Michigan and Maryland, as well as how they were affected by season, region, resource availability, tree size and crown condition. In Michigan, we quantified predation in association with EAB developmental stages on different trees over 2 years, whereas, in Maryland, we recorded woodpecker attacks on the same trees for 1 year.
 - 3 Season was a significant predictor of woodpecker predation, with most occurring in winter when late-instar larvae were abundant. Predation also was affected by crown condition and tree size. Additionally, predation levels were similar throughout the year in a region where generations are considered to be less synchronized, representing a more consistent resource for woodpeckers.
 - 4 The present study highlights the various factors affecting woodpecker predation over time. The results demonstrate the importance of multi-season studies of interactions between invasive species and native natural enemies when aiming to fully understand their dynamics.

Keywords Buprestidae, *Fraxinus*, invasive species, Picidae, predation.

Introduction

Mortality factors play a key role in the population dynamics of insect pests (Elkinton & Liebhold, 1990; Hunter *et al.*, 1997; Turchin *et al.*, 1999) and understanding them is crucial for the development of successful management programmes. Subsequent to first being detected in North America in 2002, emerald ash borer (EAB) *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) has killed tens to hundreds of millions of ash trees (*Fraxinus* spp.), causing widespread ecological damage (Ulyshen *et al.*, 2011; Flower *et al.*, 2013a; Gandhi *et al.*, 2014). Furthermore, EAB is among the most economically damaging invasive forest insects in North America to date (Aukema *et al.*, 2011) and also poses an increasing threat to ash trees in Europe

(Straw *et al.*, 2013). In its native range in northeastern Asia, EAB is a minor pest of native ash trees, and populations are regulated by innate host tree resistance and natural enemies (Liu *et al.*, 2007; Wang *et al.*, 2010; Duan *et al.*, 2012b). A lack of resistance to EAB is considered to be the primary reason that North American ash species are so severely infested by EAB (Rebek *et al.*, 2008), although there is evidence to suggest that some native natural enemies such as parasitoids (Duan *et al.*, 2012a, 2013) and woodpeckers (Piciformes: Picidae) have low to moderate impact with respect to suppressing EAB populations in North America (Cappaert *et al.*, 2005b; Lindell *et al.*, 2008; Jennings *et al.*, 2013; Flower *et al.*, 2014). Indeed, woodpeckers in particular may represent the biggest source of mortality for EAB in North America (Duan *et al.*, 2014; Lyons, 2015).

Woodpeckers have previously shown positive numerical responses to outbreaks of pest insects (Jiao *et al.*, 2008;

Correspondence: David E. Jennings. Tel.: 301 405 3635; fax: 301 314 9290. e-mail: david.e.jennings@gmail.com

Hu *et al.*, 2009; Edworthy *et al.*, 2011; Reeve, 2011) and, combined with other natural enemies, they can regulate some pest populations (Stephen & Berisford, 2011). Signs of woodpecker foraging and predation on trees also can be indicative of infestations by wood-boring beetles (Coleman *et al.*, 2011). To our knowledge, three species of woodpecker are documented as having responded to EAB in North America: downy (*Dryobates pubescens* L.), hairy (*Leuconotopicus villosus* L.) and red-bellied (*Melanerpes carolinus* L.) woodpeckers (Lindell *et al.*, 2008; Koenig *et al.*, 2013). Levels of woodpecker predation on EAB are linked to the density of EAB larvae within trees and certain site characteristics (Lindell *et al.*, 2008; Jennings *et al.*, 2013). However, previous studies have reported high variability in predation levels between trees within sites, suggesting that other biotic and abiotic factors might influence woodpecker predation. Disentangling the relative importance of these different biotic and abiotic factors is necessary for accurately parameterizing the contribution of predation in models on EAB population growth and spatial spread.

Some of the differences in woodpecker predation levels may relate to variation found in the EAB life cycle. EAB females lay eggs in bark crevices during the spring and summer and, after hatching, the first-instar larvae burrow through the bark and feed in the phloem during the summer and autumn. Larvae of EAB develop through four larval stages and, when mature, chew a pupation gallery (in the outer sapwood or bark, depending on bark thickness) in which they fold into J-shaped larvae and undergo obligatory diapause; prepupation, pupation and adult eclosion occur the next spring or summer. However, in some cases, EAB larvae will overwinter as early instars and feed throughout a second summer before reaching the overwintering J-larval stage. Thus, EAB generations can be univoltine or semivoltine (Cappaert *et al.*, 2005a, 2005c; Tluczek *et al.*, 2011), leading to considerable asynchrony between generations. This life cycle appears to be influenced by factors such as host tree condition, EAB population density and climate (Siegert *et al.*, 2010; Tluczek *et al.*, 2011), although the exact mechanisms driving the selection of life cycle remain somewhat unclear. Nonetheless, in areas where generations are less synchronized, EAB larvae/pupae may represent a more stable resource for woodpeckers throughout the year, and this could affect the temporal dynamics of their predation.

The present study aimed to examine the temporal dynamics of woodpecker predation on immature EAB, including factors affecting woodpecker predation such as season, resource availability (i.e. abundance of different developmental stages of EAB), tree size and crown condition. Accordingly, we conducted separate surveys of woodpecker predation on EAB in Michigan and Maryland, with one important distinction: in Michigan, we used destructive sampling to quantify resource availability and predation on different trees for each sample, whereas, in Maryland, we recorded predation on the same trees throughout the study and did not sample trees destructively. This approach enabled us to examine the dynamics of predation over time, as well as the potential drivers of these patterns. Given that woodpeckers appear to mostly attack older EAB larvae and pupae (Jennings *et al.*, 2013; Duan *et al.*, 2014) and that some species are more active foragers in winter (Conner, 1981), predation was predicted to be greatest in winter or spring when those EAB

life stages are typically more abundant (Cappaert *et al.*, 2005c). However, resource availability should be dependent on the synchronization of EAB populations in the region of study. For example, EAB populations in western Maryland appear to have less synchronized generations than those in southern Maryland (Jennings *et al.*, 2013). Therefore, woodpecker predation might be higher in winter and spring in areas where populations have highly synchronized generations, whereas it will be more evenly distributed across seasons when generations are not synchronized. Based on previous work (Lindell *et al.*, 2008), we also predicted that woodpecker predation would generally be highest on larger trees that were in poor condition (i.e. trees containing a greater abundance of EAB larvae/pupae).

Materials and methods

Michigan tree survey

This survey was conducted at three sites in Ingham County, Michigan: Burchfield County Park (BF: 42.570°, -84.601°), the two contiguous Central and Nancy Moore Parks in Meridian Township (CP: 42.717°, -84.417°) and Harris Nature Center and Legg Park (LP: 42.684°, -84.367°). Site characteristics are described in detail in Duan *et al.* (2012a). Briefly, these sites were mostly early successional secondary growth forests where green ash (*Fraxinus pennsylvanica* Marshall) was the dominant tree species. EAB was first discovered in the vicinity of these study sites in 2004, and ash tree mortality became evident the next year. By 2009–2010, the larger trees at these sites were heavily infested with EAB and, consequently, most of the larvae appeared to be in relatively synchronized univoltine generations.

At each sampling period, four to 15 green ash trees exhibiting signs of EAB infestation (e.g. crown decline, epicormic growth, EAB emergence holes) were selected per site to be debarked in spring, summer and autumn of 2009 and 2010. The diameter at breast height (DBH) was recorded for all trees sampled (mean \pm SE = 11.47 \pm 0.37 cm). As the trees were debarked, we counted the number of live EAB larvae in different life stages and the number of EAB larvae or pupae preyed upon by woodpeckers. Woodpecker predation on EAB was determined by examining the outer bark for characteristic holes made by these birds, which we assumed terminated in the removal of EAB larvae or pupae from galleries beneath (Fig. 1). For analysis, live EAB were grouped together into early instars (L1–L2), late instars (L3–L4) and overwintering/mature (OW) stages (J-shaped larvae, prepupae and pupae).

Maryland tree survey

This survey was conducted on trees in western and southern Maryland. In the western Maryland region, study trees were located in Allegany County (AL: 39.621°, -78.488°), whereas, in the southern Maryland region, study trees were located in Prince George's County (PG: 38.714°, -76.971°). Study trees within each region were distributed across sites of approximately 2.5 ha in area. The site in AL was located in a mixed oak (*Quercus* spp.) upland forest, with an abundance of *F. pennsylvanica* and fewer stems of *Fraxinus americana* L. In PG, the site



Figure 1 Example of a woodpecker feeding hole through the outer bark of an ash tree *Fraxinus* spp. terminating at an emerald ash borer *Agrilus planipennis* gallery beneath. Photograph credit: David E. Jennings (University of Maryland).

was located in a seasonally flooded lowland forest dominated by *F. pennsylvanica*. EAB infestations were known in AL and PG from at least 2011 and 2010 onward, respectively. Belt transect surveys (10 × 100 m) conducted in July 2013 were used to characterize the ash stands in each area by estimating ash stem density, mean crown condition, mean DBH and number of EAB emergence holes for each ash tree surveyed. Tree crown condition was assessed on a scale of 1–5 (with 1 representing a healthy tree with no crown defoliation, 2 representing a crown with slight dieback, 3 representing < 50% crown dieback with some of the top branches exposed, 4 representing a crown with > 50% dieback and 5 representing a dead ash tree without leaves), based on the work of Smith (2006) and Flower *et al.* (2013b). The study sites in both regions of Maryland were generally similar in terms of ash stem density (AL = 110/ha, PG = 150/ha) and mean DBH (AL = 14.41 ± 0.90 cm, PG = 13.58 ± 1.67 cm), and the mean crown conditions (AL = 2.05 ± 0.23, PG = 3.14 ± 0.36) indicated that both sites had relatively similar levels of EAB infestation.

In late November 2013, we randomly selected and marked a total of 90 green ash trees to study (45 in each region) and, in August 2014, we assessed the crown condition of each study tree (Table 1). Study trees were similar between regions in terms of mean crown condition (AL = 2.82 ± 0.20, PG = 3.31 ± 0.18) and mean DBH (AL = 13.00 ± 0.65 cm, PG = 13.62 ± 1.29 cm). After the trees were marked, we recorded the number of holes from woodpecker attacks on EAB larvae/pupae and number of EAB emergence holes within the lower 2.5 m of the trunk, before filling them with translucent caulk (to prevent re-counting). Surveys were conducted approximately every 3 months for 1 year, enabling us to quantify the temporal dynamics of woodpecker predation across seasons (winter: December to February; spring: March to May; summer: June to August; autumn: September to November). During each of these subsequent surveys, we again recorded and marked any new woodpecker attacks and EAB emergence holes. Trees were not destructively sampled to

Table 1 Mean ± SE diameter at breast height (DBH) by crown condition for ash trees in southern ($n = 45$) and western ($n = 45$) Maryland during the winter of 2013 through to the spring, summer and autumn of 2014 (n is given in parentheses for each crown condition)

Crown condition	AL	PG
	Mean DBH	Mean DBH
1	16.09 ± 1.33 (9)	6.54 ± 0.41 (5)
2	13.26 ± 0.79 (11)	21.98 ± 4.72 (5)
3	10.74 ± 1.21 (11)	13.25 ± 2.53 (13)
4	13.91 ± 1.97 (7)	15.45 ± 2.00 (15)
5	11.24 ± 1.36 (7)	9.81 ± 0.98 (7)

Ash trees at the sites were *Fraxinus pennsylvanica* and *Fraxinus americana*. In accordance with Smith (2006), tree crown condition was assessed on a scale of 1–5 (with 1 representing a healthy tree with no crown defoliation, 2 representing a crown with slight dieback, 3 representing < 50% crown dieback with some of the top branches exposed, 4 representing a crown with > 50% dieback and 5 representing a dead ash tree without leaves).

quantify EAB density. However, previous work on ash trees in Maryland and elsewhere has shown that crown condition is correlated with EAB larval densities (Flower *et al.*, 2013b; Jennings *et al.*, 2013).

Woodpecker diversity and abundance in Maryland

Each time that we visited sites in Maryland to quantify woodpecker predation (i.e. winter, spring, summer and autumn), we also conducted transect samples to identify the woodpecker species present at the sites and survey their abundance. Transects were conducted by walking diagonally across the sites for a duration of 30 min, and any woodpeckers observed were identified to species (with or without binoculars, as necessary). All surveys were conducted between 10.00 and 14.00 h. Because the birds were not marked, we were unable to determine whether there was more than one individual, and therefore repeated observations at a site may have been of the same individual.

Statistical analysis

All statistical analyses were conducted using R, version 3.1.2 (R Core Team, 2014). For the Michigan survey, we evaluated the effects of season, site, tree DBH and sampling year on the number of woodpecker attacks per tree (calculated as the number of woodpecker attacks/total number of EAB per tree). Because sampling was not conducted during winter in Michigan, the spring sample was assumed to also include winter predation (hereafter referred to as winter–spring for the Michigan data). We also investigated how season interacted with site, tree DBH and sampling year. Proportions of woodpecker attacks were fitted to a generalized linear model with a binomial distribution (Warton & Hui, 2011). Significance was then assessed using likelihood ratio (LR) chi-square tests with type II sums of squares. To examine how numbers of EAB in different life stages varied with season, we first controlled for differences in tree size by estimating the phloem area of trees with a second-order polynomial model based on tree DBH (McCullough & Siegert,

2007). EAB numbers were then converted to counts per unit area (m^2) of phloem, and data were fitted to generalized linear models with quasi-Poisson distributions (O'Hara & Kotze, 2010). These were followed by Tukey's honestly significant difference tests when significant effects of season were found ($P < 0.05$).

For the Maryland survey, we looked at the effects of season, region, tree DBH and crown condition on the number of woodpecker attacks per tree. We used crown condition in the models because we found that it was highly correlated with the number of EAB emergence holes (Spearman's $\rho = 0.610$, $P < 0.001$). Numbers of woodpecker attacks were converted to counts per unit area (m^2) of bark surface area (i.e. we sampled only the lower 2.5 m of trees) and data were fitted to a generalized linear model with a quasi-Poisson distribution (O'Hara & Kotze, 2010), with significance assessed by using LR chi-square tests with type II sums of squares. Fisher's exact test was used to compare woodpecker abundance between season and region.

Results

Michigan tree survey results

In 2009/2010 (as EAB densities peaked at the study sites), the overall mean percentage of EAB preyed upon by woodpeckers per tree was $35.2 \pm 2.1\%$, with a maximum of 88.2% mortality from woodpeckers found on a single tree. Season interacted with year and DBH to affect the level of woodpecker predation on trees in Michigan at peak EAB densities (Table 2). Most woodpecker predation was in winter–spring in 2009, although this shifted to autumn in 2010 (Fig. 2a). Additionally, we found that woodpecker predation was negatively associated with tree DBH in winter–spring and summer but positively associated with DBH in autumn (Fig. 2b).

Season significantly affected the number of live EAB/ m^2 in overwintering/mature stages (LR: $\chi^2 = 18.10$, d.f. = 2, $P < 0.001$) but not the number of early (LR $\chi^2 = 1.28$, d.f. = 2, $P = 0.529$) or late instars (LR: $\chi^2 = 0.33$, d.f. = 2, $P = 0.849$). The number of early- and late-instar EAB larvae was generally similar across winter–spring, summer and autumn, although overwintering/mature stages were almost exclusively found in winter–spring and autumn, with very few found in the summer (Fig. 3). Indeed, Tukey's honestly significant difference revealed that there were significantly fewer EAB in overwintering/mature stages in summer compared with winter–spring ($P < 0.05$).

Maryland tree survey results

We were unable to collect data from two trees for the autumn sample because they had been cut down by North American beavers (*Castor canadensis*) at some point after the summer sampling. In 2013–2014, 22 of the trees (25%) that we selected received no woodpecker predation on the lower 2.5 m of trunk. Of the trees receiving no predation, eight had a crown condition of 1, with the remaining 14 trees exhibiting various stages of crown decline. In addition, these trees were across all sizes and, although they were found in both regions, most were in AL.

Overall, we found that most woodpecker attacks occurred in winter; fewer occurred in autumn and summer, and the fewest

Table 2 Generalized linear model (binomial error distribution) of factors affecting woodpecker predation on emerald ash borer in ash trees sampled and debarked at three study sites in southern Michigan during the spring ($n = 45$), summer ($n = 24$) and autumn ($n = 54$) of 2009 and 2010

Factor	LR χ^2	d.f.	<i>P</i>
Season	20.83	2	< 0.001
Site	1.71	2	0.426
Year	0.15	1	0.695
DBH	0.92	1	0.339
Season \times Site	6.83	4	0.145
Season \times Year	20.10	2	< 0.001
Season \times DBH	9.09	2	0.011

DBH, diameter at breast height. Significant factors are shown in bold.

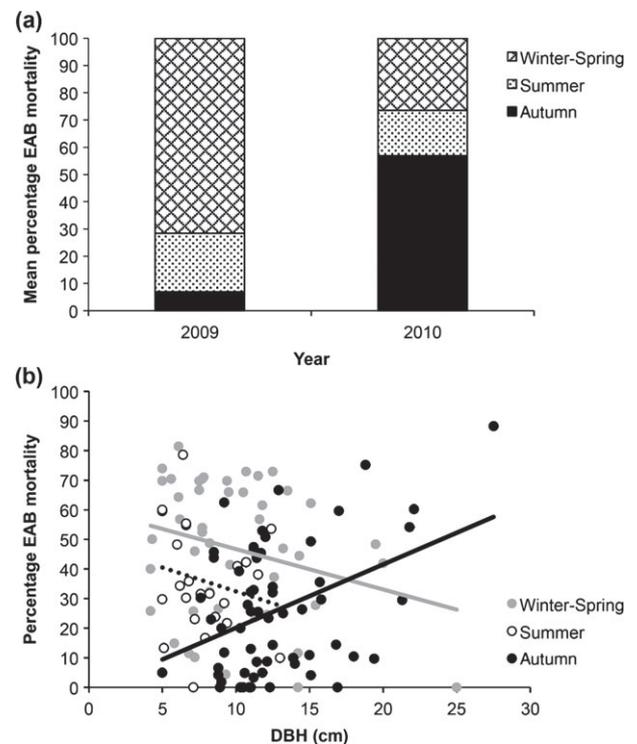


Figure 2 Mean percentage mortality of emerald ash borer (EAB) *Agrilus planipennis* from woodpecker predation by sampling year and season (a) and percentage mortality from woodpecker predation per tree by diameter at breast height (DBH) and season (b), in southern Michigan in 2009–2010, when EAB densities peaked.

were observed in spring (Fig. 4a and Table 3). The number of woodpecker attacks was negatively associated with DBH (Table 3) and there were significant interactions between season and region (Fig. 4a and Table 3), as well as season and crown condition (Fig. 4b and Table 3), on woodpecker predation in Maryland. In southern Maryland (PG), most woodpecker attacks occurred during winter, with comparatively few during spring. Conversely, although most woodpecker attacks still occurred in winter in western Maryland (AL), the numbers found in spring were similar to those found in summer and autumn. For the interaction between season and crown condition, we found that

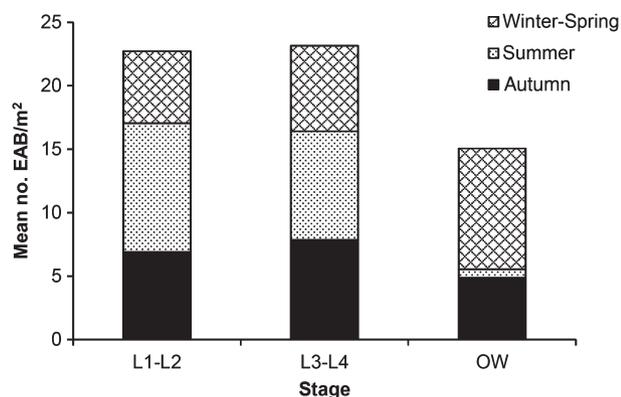


Figure 3 Mean number of live immature emerald ash borers (EAB) *Agilus planipennis*/m² of phloem in trees by season in Michigan (2009–2010). Categories are: L1–L2 (early-instar larvae, $n=1886$), L3–L4 (late-instar larvae, $n=2124$) and OW (overwintering stages: J-larvae, prepupae and pupae, $n=1703$).

woodpecker predation on unhealthy trees was higher in winter compared with other seasons (Table 3).

Woodpecker diversity and abundance in Maryland

Woodpeckers were observed a total of 21 times during our surveys (Table 4) and we identified three species of woodpecker in the study sites (downy, hairy and red-bellied). Combining both regions together, downy woodpeckers had the highest relative abundance (71.4%), followed by hairy (19.1%) and then red-bellied (9.5%). Taking a more conservative approach (given that individuals may have been recounted during surveys) and only considering species presence/absence, downy woodpeckers (observed during six sampling periods) were still observed in surveys more often than hairy (two) or red-bellied (two) woodpeckers. Woodpecker abundance was similar between regions in spring and summer and, although abundance was quite different between regions in winter and autumn, it was not significant (Fisher's exact test, $P=0.054$).

Discussion

The results of the present study showed that the temporal dynamics of woodpecker predation on EAB were affected by season, crown condition and tree size, and that this pattern was likely driven by resource availability. Across surveys in Michigan and Maryland, most woodpecker predation generally occurred on trees in winter (when late-instar larvae were most abundant), and with deteriorating crowns. This was consistent with our hypotheses and similar to the results of previous work reporting that woodpecker predation was correlated positively with EAB density (Lindell *et al.*, 2008; Jennings *et al.*, 2013). Nonetheless, similar to Lindell *et al.* (2008), we found that the relationship between woodpeckers and EAB is complex, with some unhealthy trees that were presumably heavily infested with EAB experiencing no signs of foraging by woodpeckers.

Season is known to influence woodpecker foraging behaviour, particularly with respect to the feeding methods (e.g. depth of

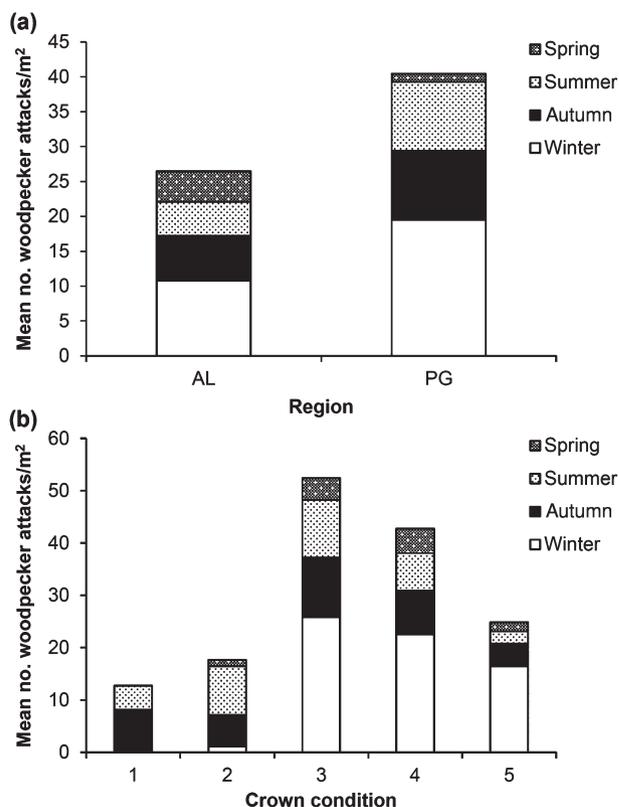


Figure 4 Mean number of woodpecker attacks/m² on the lower 2.5 m of ash trunks ($n=88$) by season and region (a) and season and crown condition (b) at sites in southern Maryland (PG) and western Maryland (AL), with data pooled for display purposes. In accordance with Smith (2006), tree crown condition was assessed on a scale of 1–5 (with 1 representing a healthy tree with no crown defoliation, 2 representing a crown with slight dieback, 3 representing < 50% crown dieback with some of the top branches exposed, 4 representing a crown with > 50% dieback and 5 representing a dead ash tree without leaves).

excavations), microhabitats used (e.g. tree size, foraging height on tree) (Jackson, 1970; Conner, 1981) and duration of foraging events (Pechacek, 2006; Czeszczewik, 2009). Previous studies found differences in levels of woodpecker foraging activity by season. For example, in China, great spotted woodpeckers (*Dendrocopos major* L.) preyed upon Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky) larvae and pupae more frequently in winter and spring (Hu *et al.*, 2009). However, seasonal effects on foraging can be highly dependent on the species of woodpecker studied. For example, pileated woodpeckers, *Hylatomus pileatus* L., increase the breadth of microhabitats used in winter compared with warmer months, whereas other species such as hairy woodpeckers tend to use a narrower range of microhabitats in winter (Conner, 1981).

We found some support for the hypothesis that levels of woodpecker predation can be influenced by the synchronization of EAB generations. Specifically, in western Maryland (AL), more predation was observed in spring, and overall levels of predation were more similar throughout the year in this region. This observation is consistent with the hypothesis that EAB generations in this cooler region of Maryland are less synchronized

Table 3 Generalized linear model (quasi-Poisson error distribution) of factors affecting woodpecker predation on emerald ash borer in ash trees at study sites in southern ($n = 45$) and western ($n = 45$) Maryland during the winter of 2013 through to the spring, summer and autumn of 2014

Factor	LR χ^2	d.f.	<i>P</i>
Season	53.99	3	< 0.001
Region	3.21	1	0.073
Crown condition	36.52	4	< 0.001
DBH	14.66	1	< 0.001
Season \times Region	14.47	3	0.002
Season \times Crown condition	41.94	12	< 0.001
Season \times DBH	2.13	3	0.547

DBH, diameter at breast height. Significant factors are shown in bold.

and present a more consistent resource for woodpeckers. By contrast, in southern Maryland (PG), which is warmer, we found that woodpecker predation was much higher in winter and lower in spring. In addition to climate, tree health could have influenced the synchronization of generations, with healthier trees possibly delaying the maturation of some EAB larvae. Although the timing of sampling prevented us from distinguishing predation between winter and spring in Michigan, the higher level of woodpecker predation on EAB in the combined winter–spring period compared with autumn and summer also adds support to the idea that EAB generations at these sites were highly synchronized.

It was not surprising that crown condition was a significant predictor of woodpecker predation in Maryland because of its high positive correlation with EAB density (Flower *et al.*, 2013b; Jennings *et al.*, 2013). In areas with known EAB infestations, ash trees with deteriorating crown conditions tend to have a higher density of EAB. This observation is consistent with the suggestion by Jennings *et al.* (2013) that woodpeckers are not likely to noticeably impact low density populations of EAB. It remains to be seen how woodpecker predation on high density populations of EAB interacts with parasitism from other natural enemies to potentially regulate EAB populations, although evidence indicates that, at the very least, woodpecker predation does not prevent biological control agents from establishing (Duan *et al.*, 2015). Woodpecker attacks were also observed on EAB in ash trees with no leaves. Ash trees in poor condition can still experience high levels of EAB oviposition (Jennings *et al.*, 2014) and, given that our assessment of crown condition did not occur until towards the end of the summer, it is likely that those trees could still have contained some live J-larvae by the time of the autumn sampling.

There was mixed support for the hypothesis that woodpecker predation would be higher on larger trees. We found a significant interaction between DBH and season in Michigan but a negative relationship between the number of woodpecker attacks/m² and DBH in Maryland. The interaction in Michigan could indicate different behavioural responses by woodpeckers to EAB abundance in trees at heavily infested sites with established populations of the beetle. That we did not observe the same trends with DBH in both surveys might reflect the fact that the EAB infestation was at an earlier stage in the Maryland sites compared with those in Michigan (potentially resulting in differences in ash basal area) or that we only examined the lower 2.5 m of trees in Maryland. Alternatively, this variation between

Table 4 Number of woodpeckers observed by region and season in Maryland

Season	Region					
	AL			PG		
	DO	HA	RB	DO	HA	RB
Winter	4	0	1	1	0	0
Spring	0	2	0	2	0	0
Summer	1	2	0	3	0	0
Autumn	0	0	0	4	0	1
Total	5	4	1	10	0	1

Regions: western Maryland in Allegany County (AL) and southern Maryland in Prince George's County (PG). Woodpecker species: DO = downy, *Dryobates pubescens*; HA = hairy, *Leuconotopicus villosus*; and RB = red-bellied, *Melanerpes carolinus*. Birds were not marked and therefore repeated observations at a site may have been of the same individual.

surveys could stem from the species-specific foraging rates of woodpeckers on EAB not being quantified. Indeed, although certain species such as hairy woodpeckers might preferentially select smaller trees to forage on, other species of woodpecker and bark-foraging birds that were not observed (e.g. pileated woodpeckers) might prefer larger trees. For example, Petit *et al.* (1988) found that woodpecker predation on red oak borers (*Enapholodes rufulus* Haldeman) occurred more often in trees with smaller DBH. Additionally, McCann and Harman (2003) found that hairy woodpeckers preferred small, unhealthy trees when foraging for locust borer (*Megacyllene robiniae* Forster) larvae.

The sampling in Maryland did not indicate that woodpecker populations were positively responding numerically to EAB. However, our sampling was not as exhaustive spatially or temporally as other research (Koenig *et al.*, 2013), which might have limited our ability to detect such patterns. The lack of a numerical response by woodpeckers could also have resulted from the number of live ash still present in the study sites, which might limit nesting habitat for these birds, as well as the availability of EAB prey. With time, as the EAB infestation accelerates and more trees start to die, a woodpecker aggregation response might be observed.

The results of the present study demonstrate the importance of multi-season studies of interactions between invasive species and native natural enemies with respect to fully understanding their dynamics. More specifically, they might help to parameterize models predicting EAB population growth and dispersal. For example, some life table analyses of EAB have utilized data collected from larvae in the autumn and, consequently, these studies have needed to estimate woodpecker predation for the remainder of the winter and spring (Duan *et al.*, 2014). The results from the present study should enable a more accurate estimation of woodpecker predation for such work, although they are somewhat limited by the relative lack of temporal replication. Longer-term studies could help to clarify the true nature of how season and tree size affect woodpecker predation on EAB. Future research should also examine the effects of spatial relationships between trees, as well as forest community composition, on woodpecker predation of EAB.

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