



Host condition effects upon *Agrilus planipennis* (Coleoptera: Buprestidae) captures on decoy-baited branch traps

MICHAEL J. DOMINGUE¹, JENNIFER BERKEBILE², KIM STEINER², LOYAL P. HALL¹, KEVIN R. CLOONAN¹, DAVID LANCE³ and THOMAS C. BAKER¹

¹ The Pennsylvania State University, Department of Entomology, 120 Chemical Ecology Lab, University Park, PA 16802, USA; e-mails: mjd29@psu.edu, lph1@psu.edu, krc204@psu.edu, tcb10@psu.edu

² The Pennsylvania State University, Department of Ecosystem Science and Management, University Park, PA, USA; e-mails: jen.berkebile@gmail.com, kcs@psu.edu

³ United States Department of Agriculture, Animal and Plant Health Inspection Service, Plant Protection and Quarantine, Buzzards Bay, MA, USA; e-mail: David.R.Lance@aphis.usda.gov

Key words. Coleoptera, Buprestidae, *Agrilus planipennis*, emerald ash borer, exit hole, flight, invasive species, mate search, phenology

Abstract. We deployed branch traps in an ash (*Fraxinus*) plantation to investigate how *Agrilus planipennis* behavior is associated with *Fraxinus pennsylvanica* condition and dispersal patterns. Data were collected from traps with or without the presence of beetle visual decoys, and from a yearly survey of exit holes. The traps were placed on trees that were either clearly declining, with most foliage arising from epicormic sprouting, or on apparently healthy trees, with little evidence of damage or decline. We calculated correlations of exit holes among neighboring tree rings and also between exit holes and male trap captures. The damaged trees the traps were hung upon had more cumulative exit holes observed than the corresponding healthy trees. However, there was otherwise no evidence that the experiment was biased by differences in exit hole patterns of the surrounding trees. Male captures were greater on decoy-baited traps than controls and this decoy effect was most clearly apparent late in the season when traps were placed on healthy trees. There were also patterns of correlations between male captures and exit hole numbers that may be indicative of short-range mate finding-and dispersal behaviors. Female captures were sparser, but were positively affected by decoys on healthy and declining trees early in the season. Thus, the results suggest that the placement of such traps on healthier trees will maximize detection, and the branch traps also show promise for further use in dispersal studies.

INTRODUCTION

Ever since the earliest detection of the emerald ash borer *Agrilus planipennis* Fairmaire in North America by visual inspection of infested ash trees (Haack et al., 2002), there has been a concerted effort to improve detection methods for this and other potentially harmful invasive buprestid beetle species. The failure to find a highly attractive long-range pheromone has led to a research focus upon trapping technologies that maximize short-range attraction to visual and chemical cues. For example, it was determined that green or purple coloration for large sticky panel traps optimizes trap captures (Francese et al., 2005, 2010a). Furthermore, the size and structure of such color-dependent traps have been progressively improved (Francese et al., 2008, 2010b, 2011), and have been evaluated at different population densities (Marshall et al., 2010; Francese et al., 2013; Poland & McCullough, 2014).

The existing trap technologies have been further improved by emitting tree odors from the trap (Crook et al., 2008, 2012; Grant et al., 2010), and an *A. planipennis*

pheromone component, (3Z)-dodecen-12-olide (Silk et al., 2011). The highly variable and relatively modest increases in captures from the pheromone in comparison to long-range pheromones of other species suggest that it is likely only active at close range. It has also been determined that placing (Z)-3-hexen-1-ol and pheromone baited traps on southern facing branches in sunlight strongly increases the captures of males (Ryall et al., 2015), further indicating that localized factors are critical for optimal trapping of this species.

Another trapping approach undertaken during some of the earliest years of *A. planipennis* detection research involved using visual decoys of beetles on smaller surfaces to elicit the visual mate-behavior that males normally exhibit toward females resting on ash leaves (Lelito et al., 2007). Initially this approach consisted of pinning dead females to single sticky ash leaflets (Lelito et al., 2008). More recently, artificial surfaces (5 × 10 cm green sticky cards) and nanofabricated visual decoys have been incorporated into the design of such traps, which are affixed to the ends

of single ash branches and have been called “branch traps” (Domingue et al., 2013b, 2014, 2015). Although these small branch traps have demonstrated that decoy beetles can significantly attract *A. planipennis* males and males of several other *Agrilus* species, optimal deployment procedures have not been developed, nor has this type of trap been evaluated at a range of *A. planipennis* population density conditions. Thus, many questions remain concerning the viability of such traps as an alternative to commonly used technologies.

One specific concern for any trapping design is whether the success of detection in using a particular trap type is dependent upon their fortuitous placement in or near highly infested areas. Such areas might include the sites of spring adult emergence or preferred oviposition. This may be a particular concern for species such as *A. planipennis*, which are known to begin their feeding and mating activity high in the canopy before progressing downward in successive years as the tree declines (Cappaert et al., 2005). In daily trap capture counts of branch traps containing visual decoys it was observed that a strong increase in male attraction occurred approximately three weeks after the first beetles were detected (Domingue et al., 2015). Thus the traps appeared to be most effective in attracting males well after their initial emergence from trees. However, it is conceivable that the placement of some traps on or near trees experiencing high beetle emergence could have influenced the results. Even though most traps had been placed on healthier trees without many emerging beetles, it was noted that one particular trap placed on a tree with many new exit holes had a strongly elevated capture rate (Domingue et al., 2015).

Two objectives were thus pursued using a single experiment that deployed branch traps on healthy versus damaged trees in a heavily infested ash plantation in Pennsylvania. The first was to simply elucidate whether the branch traps are effective at capturing locally dispersing beetles when placed on healthier trees, or if they only perform well when placed on heavily damaged trees that are likely to have many beetles emerging from them. This information is important for assessing the potential of these traps as useful monitoring tools. The second objective involved inferences about the patterns of male and female movements within the plot. The second objective was accomplished by considering trap placement in the context of an exit hole survey of all the trees. These data provide information about sources of emerging adults and tree conditions that can be used in conjunction with trap characteristics and locations to infer behavioral tendencies exhibited by beetles within the plot.

MATERIALS AND METHODS

Field site

Traps were deployed on May 25, 2014 at a site on the Pennsylvania State University campus in University Park, PA, (40.810398N, 77.8427868W, 318 m altitude). The site was previously used for other branch trap experiments for *A. planipennis* (Domingue et al., 2015). The site consisted mostly of green ash, *Fraxinus pennsylvanica* Marshall, uniformly planted in 1978

from populations representing the entire natural distribution of the species (Steiner et al., 1988). There were originally approximately 2000 trees arranged in rows and columns at a spacing of 3.7 m. In 2013 at the time of our first trapping experiment at the site, the mortality was at 10–15% (Domingue et al., 2015). By early in the summer of 2014, the mortality had increased to 51.4%. Through most of the site there were 20 rows of trees on a north-south uphill gradient with a 15 m elevation rise. There was a 20-m-wide grassy field separating the eastern ~40% and western ~60% of the trees.

A total of fourteen trees were selected for placement of traps. Six of these trees were healthy with no signs of decline due to *A. planipennis* infestation. The remaining eight trees were experiencing strong symptoms of dieback, including death of most of the crown and a significant amount of epicormic sprouting. These trees were selected such that each “healthy” tree was within approximately 10 m of one of the “declining” trees. This element of the design was implemented in an effort to preclude potential biases arising from differing localized population densities within the plot. The discrepancy in the number of traps on health and declining trees occurred because it was not possible to locate more than six non-neighboring healthy trees that matched the criterion of having low enough sun-lit branches to hang branch traps upon.

Branch traps

The branch traps were constructed from halved, inverted white delta traps (ISCA Technologies), as described in detail elsewhere (Domingue et al., 2013b, 2015). Each trap was fastened around a leaf cluster with clips such that its two 5 × 9 cm² green sticky surfaces were oriented toward the sun at approximately 45° in comparison to the ground. Traps were always placed on the south-facing tree branches, exposed to direct sunlight for most of the day, approximately 1.5–2.5 m from the ground.

Within each of the trees selected for monitoring, two traps were placed on neighboring branches typically at 1–2 m apart. The branches were either lower exposed branches of healthy trees, or large epicormic sprouts from the declining trees. One of each of the traps were left with no decoys as a control. The other of the two traps on each tree was baited with a visual decoy by pinning an *A. planipennis* specimen to the center of both green cards. *A. planipennis* specimens used as visual decoys were provided by the APHIS rearing facility in Brighton, MI. There were thus 8 decoy and 8 control traps on “damaged” trees, while there were 6 decoy and 6 control traps on “healthy” trees.

The green plastic surfaces of the traps, including any decoys, were sprayed with a thin coating of Tanglefoot™. Although (Z)-3-hexen-1-ol dispensers were previously added in experiments using these traps (Domingue et al., 2014, 2015), no odor lures were added for this experiment. It is possible that healthy and declining trees emit different volatiles, which may affect *A. planipennis* attraction. Thus any additional application of odors might interfere with such potential effects, and thus impact the ability to assess our experimental objectives. The branch traps were deployed on May 28, 2014 and monitored daily until July 11, 2014, when there had been three successive days with no captures. The traps were then monitored weekly for the rest of the season, with only 2 captures occurring past July 11.

Exit hole survey

Agrilus exit holes can readily be observed on the boles of infested trees, and a random sample of such holes from the bole has been shown to be a good indicator of the total number of adults for another species (Haavik et al., 2012). In this plantation, from 2012 to 2014, a yearly survey had been conducted of the exit holes visible between 1.25 and 1.75 m high on the trunk of each tree. Because the exit hole surveys were conducted yearly, a

comparison of new exit holes versus cumulative exit holes from *A. planipennis* emergence was made in 2014, to coincide with the trapping experiment. New exit holes from 2014 were calculated simply by subtracting the cumulative exit holes observed in 2013 from those observed in 2014 on each tree.

For considering the spatial aspect of exit hole patterns on trees surrounding a trap, we tabulated the data in successively larger rings around the tree of interest. We use the notation of degrees to describe the distance of each ring from the tree the trap is hung upon (Fig. 1). The tree itself is thus designated as the 0° ring (Fig. 1A), while the 3-tree × 3-tree ring of trees around it is the 1° (Fig. 1B). Exit holes successively larger perimeters were calculated (2°, 3°, 4° shown in Fig. 1C–E) including rings up to 10°.

By selecting healthy and declining trees near each other, we hoped to avoid biases with respect to the characteristics of the surrounding trees. To assess the degree of any such bias, we compared the mean new exit hole and cumulative exit hole values for each of the rings of trees surrounding healthy and declining trees. We examined exit hole correlations between rings of trees surrounding the traps to further evaluate the degree to which new exit hole and cumulative exit hole might be spatially clustered within the plot.

Even if a bias does not exist between the exit hole patterns surrounding healthy and declining trees, there may be additional effects of the exit hole distribution patterns upon trap captures. For example, high new exit holes might be correlated with captures not only on a tree a trap was placed upon, but also in larger blocks of trees surrounding a trap. Thus, we also calculated the Pearson correlation coefficients for new exit holes and cumulative exit holes versus male trap captures for each of the treatment combinations in successively larger blocks around the traps. We did not consider females, because very few were caught overall. We also separated the data based upon whether a decoy-baited trap or a blank trap was used, and whether or not the captures were early or late in the season. The use of time period as a factor is based on previous experiences of observing changes in the middle of the flight season with respect to male and female attraction to traps (Domingue et al., 2015), which again appeared in a preliminary analysis of the 2014 experiment. The data was thus separated into an early period (May 31 to June 19) and a later period (June 20 to July 11). For each trap, we pooled all daily captures across these time periods. Additionally, we correlated the numbers of male beetles in each trap treatment with the new exit holes and cumulative exit holes summed for all rings within a given size. For example, a 4° block as shown in Fig. 1E would include the tree the trap was hung upon and all the trees within (0° to 4°). Thus while the 4° ring in Fig. 2E would have 150 new exit holes, the corresponding 4° block would have 405 new exit holes.

Handling of specimens

All specimens were placed in plastic bags during each day's collection and labeled specifically to each trap and collection date. They were frozen before the Tanglefoot glue was removed to facilitate identification. To remove the Tanglefoot glue, the specimens from each trap capture event were placed in a vial with Histoclear (National Diagnostics, Atlanta, GA, USA) for 24 h. At the end of this period, the vials and the specimens were separated and successively rinsed with hexane, acetone, and ethanol before being recombined with 2 ml of 80% ethanol for preservation. Nearly all buprestids were *A. planipennis*, but some of the smaller twig-boring species *A. subcinctus*, were also found and collected. In a previous year (Domingue et al., 2015), it was determined that this species appeared earlier in the season. Because of the fewer numbers of *A. subcinctus*, and the likelihood that the traps were deployed after the earliest flight period of this species, they were

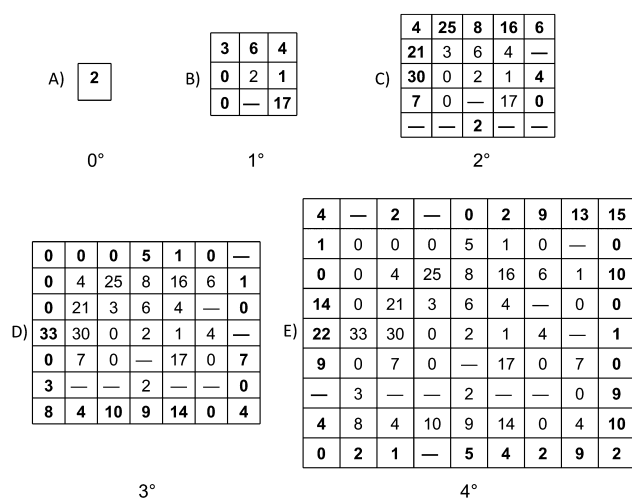


Fig. 1. Example of calculation of cumulative exit hole values for rings of trees surrounding a trap. Each cell of the grid marks the exit holes measured for a tree, and those relevant to the ring of interest are in bold. Cells marked with a hyphen represent dead trees that had been removed. Only the tree the trap is hung upon has 2 cumulative exit holes and is represented by 0° (A). The next larger ring is three trees by three trees wide and represented by a 1° model, where there are 31 cumulative exit holes (B). Progressively larger rings are shown a 2° ring where there are 123 cumulative exit holes (C), a 3° ring where there are 99 cumulative exit holes (D), a 4° ring where there are 150 cumulative exit holes (E). Exit holes for larger 5° to 10° rings were also similarly counted for each trap (not shown) with respect to cumulative exit holes and also 1° to 10° rings were counted for new exit holes.

not included in any analyses. Individual *A. planipennis* collected were also dissected to examine the genitalia so that sexual identity could be assigned to each specimen.

Statistical analyses

For the branch traps, a cumulative logit model (McCullagh & Nelder, 1989) was used to evaluate the effects of decoy presence, tree condition (declining or healthy), and time period (early versus late) of collection. Proc GENMOD in SAS version 9.2 2008 (SAS institute, Cary, NC, USA) was used for these calculations. The model was used twice to separately explore these effects on captures of male and female *Agrilus planipennis*. All binary interactions of the three experimental factors were also considered in the models for predicting male and female trap captures. The cutoff between the early versus late time period was defined at June 19, as described above. The REPEATED option in Proc GENMOD was used to account for the nesting of traps with and without decoys in the same tree. For other analyses in involving exit holes, Pearson correlations and paired t-tests were calculated using Microsoft Excel.

RESULTS

Tree condition effects on captures

Trap captures of male *A. planipennis* (N = 85) were significantly influenced by decoys and the interaction of tree condition and time period (Table 1). Examining the data more closely, it is apparent that males were particularly attracted to decoy-baited traps located on healthy trees late in the season (Fig. 2). Although males were attracted preferentially to traps with decoys rather than control traps early in the season, the attraction to the decoy-baited traps on the healthy trees later in the season was several magnitudes greater.

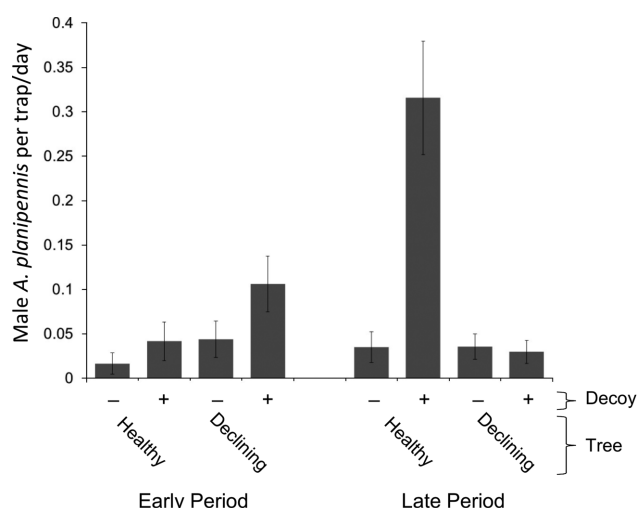


Fig. 2. Mean (\pm SE) daily male captures of *Agrilus planipennis* in the earlier trapping period (May 31 to June 19) versus the later period (June 20 to July 11) on branch traps for four trap treatments. The treatments included placement on healthy or declining trees with or without decoys.

Overall, there were fewer female captures ($N = 60$) than male captures. Furthermore, we do not show the daily captures of females or any analyses with respect to exit holes, because no easily interpretable patterns emerged. However, there were significant effects of decoy and the decoy* tree condition interaction (Table 1, Fig. 3), which indicates a greater decoy effect on healthier trees.

Exit hole patterns

The mean number of cumulative exit holes of the declining trees that traps were placed upon was significantly greater than that of the corresponding healthy trees (Table 2). However, the mean number of new exit holes did not differ between the declining and healthy trees. Furthermore, there were no differences in cumulative exit holes or new exit holes in any of the 1°–10° rings around the healthy versus declining trees. Also, the correlations between the cumulative exit hole or new exit hole values of the tree the trap was hung upon (0°) and those of the surrounding rings (1°–10°) were always relatively small (first row and column of Table 3).

There was evidence of clustering of trees according to cumulative exit holes, because 27 of the 50 correlations calculated among rings were positive and large enough to be considered significant (Table 3). While we do not claim significance for any one of these correlation coefficients, because the p -values were not corrected for the multiple

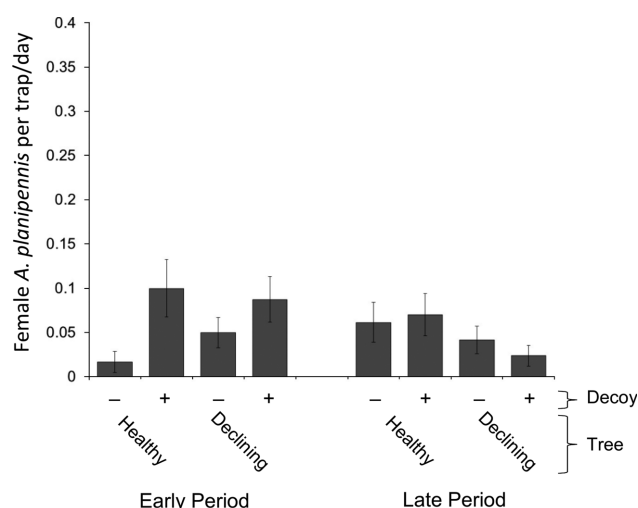


Fig. 3. Mean (\pm SE) daily female captures of *Agrilus planipennis* in the earlier trapping period (May 31 to June 19) versus the later period (June 20 to July 11) on branch traps for four trap treatments. The treatments included placement on healthy or declining trees with or without decoys.

comparisons made, they are indicative of a pervasive high degree of correlation in the plot. Furthermore, these correlations tended to be highest among the larger rings, which included the data for large numbers of adjacent trees. Overall, the mean correlation coefficient among all rings was 0.51 for cumulative exit holes. However, the Pearson correlation among new exit holes was only on average 0.10, with far fewer of the correlations between the rings reaching the significance threshold. Of the 50 correlations between rings for new exit holes, only six were positive and above this threshold, while three were negative and below the significance threshold. Thus, the infestation at the plot appears to be at a stage in 2014 where, despite localized variations in cumulative damage, current beetle emergence from living trees was not strongly clustered.

Exit hole correlations with branch trap captures

The correlations between new exit holes and trap captures were nearly always positive, but rarely above the significance threshold. This tendency occurred regardless of the size of the block of trees around the trap, whether a

Table 2. Comparison of the number of new and cumulative exit holes in 2014 observed on the six healthy trees and eight declining trees upon which branch traps were deployed (first row), as well as exit holes in successively larger rings of neighboring trees.

Area (trees)	New exit holes (2014)		Cumulative exit holes	
	Healthy	Declining	Healthy	Declining
0°	1.2 \pm 0.8	2.5 \pm 2.1	1.2 \pm 0.8	13.9 \pm 3.6*
1°	5.3 \pm 2.7	13.1 \pm 3.0	36.3 \pm 14.1	44.9 \pm 9.6
2°	21.7 \pm 6.4	24.9 \pm 4.8	76.2 \pm 26.5	93.5 \pm 19.2
3°	25.3 \pm 7.5	45.3 \pm 11.1	99.0 \pm 25.24	124.1 \pm 19.6
4°	28.5 \pm 10.6	42.6 \pm 12.8	93.3 \pm 29.3	113.9 \pm 24.0
5°	39.7 \pm 8.7	48.3 \pm 7.7	142.3 \pm 35.4	150.0 \pm 30.6
6°	37.2 \pm 19.2	51.8 \pm 5.9	115.7 \pm 45.0	163.5 \pm 47.6
7°	59.3 \pm 11.7	38.1 \pm 7.1	170.5 \pm 41.5	144.1 \pm 42.1
8°	69.8 \pm 21.6	58.4 \pm 10.6	208.5 \pm 44.3	203.8 \pm 49.3
9°	83.0 \pm 21.6	60.5 \pm 11.7	241.5 \pm 54.7	213.6 \pm 46.4
10°	68.9 \pm 12.9	62.9 \pm 13.1	224.6 \pm 63.3	234.4 \pm 50.2

* Exit hole numbers in healthy and declining trees in only this block differ using a one-tailed heterostedastic t -test, $\alpha < 0.05$.

Table 1. Summary of the cumulative logit model analysis of the effects of season, tree condition, and decoy on capture of male and female *Agrilus planipennis*.

Effect	DF	Males trap captures		Females trap captures	
		X ²	p	X ²	p
Period	1	2.70	0.1004	0.05	0.8257
Condition	1	0.02	0.8974	0.22	0.6423
Decoy	1	7.21	0.0072	4.83	0.0280
Period*Condition	1	5.93	0.0149	3.35	0.0673
Condition*Decoy	1	1.99	0.1581	5.91	0.0151
Period*Decoy	1	0.19	0.6624	2.37	0.1240

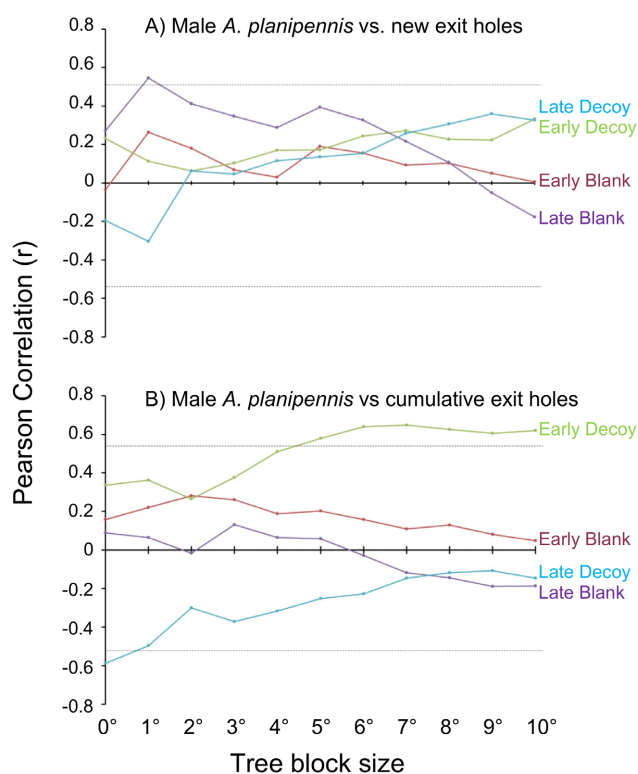


Fig. 4. Pearson correlations between number of exit holes on progressively larger groupings of trees surrounding the targeted trap (0° to 10 blocks) and its male captures. Correlations were calculated separately based upon whether there were decoys on the traps and whether they were deployed early vs. late in the season. The analysis was repeated using new exit holes counted in 2014 (A) and cumulative exit holes (B). The dotted line indicates the level at which any individual Pearson correlation would be significant at $\alpha = 0.05$, d.f. = 12.

decoy was on the trap, or whether early or late season data were considered (Fig. 4a). This data thus suggests a modest effect of new emergence upon male trap captures from all trees within 10 tree lengths of the trap. A more complicated pattern that stands out within this general trend exists for the captures of males late in the season on the blank traps. The correlation with new exit holes for this treatment were high in smaller blocks of trees, but declined and became less than zero as larger and larger blocks were considered. Likewise, a reversed pattern occurred for the late season decoy-baited traps, with the correlations increasing with

block size, albeit at a lower magnitude that never became significant.

Total cumulative exit holes had little correlation with captures of males on blank traps, regardless of whether early or late season captures were considered (Fig. 4B). However, decoy-baited traps had distinctive late and early season patterns of correlations with cumulative exit holes. Early in the season, captures of males on decoy baited branch traps were correlated best with cumulative exit holes from larger blocks surrounding the trap. For this treatment, all coefficients became significant above a 5° block size. However, late in the season, there were large negative correlations between male decoy-baited trap captures in smaller blocks, which increased as the block sized considered increased and became close to zero.

DISCUSSION

The branch traps were clearly most successful at detecting *A. planipennis* males when supplemented with a visual decoy and when deployed later in the season on the healthy trees (Fig. 2). It is also clear that these increased captures were not simply the result of the fortuitous placement on or near trees with more beetles emerging, because new exit hole values did not differ significantly between the selected trees of these two types, or when considering the surrounding rings of trees. The large negative correlations between the trap captures and cumulative exit holes on decoy baited traps late in the season, using 0° and 1° blocks for the model, also suggests that males are heavily searching for females in single trees or small clusters of trees that have remained healthy within the infestation. This interpretation follows from the likelihood that an increase in cumulative exit holes is indicative of the deterioration of tree condition. Although these effects were not as dramatic for females, the traps on healthier trees with decoys did capture the largest number of females both early and late in the season. Thus, when deploying these branch traps, placing them upon the healthiest trees available appears to be the most effective way of maximizing detection ability, perhaps even in forests which are not yet known to be infested with *A. planipennis*, but where other causes of decline may exist.

Table 3. Pearson correlation coefficients of exit holes between rings of trees surrounding traps (new exit holes above diagonal, cumulative exit holes below).

Ring	0°	1°	2°	3°	4°	5°	6°	7°	8°	9°	10°
0°	–	0.180	0.391	–0.042	–0.133	0.066	0.250	–0.185	–0.104	–0.209	–0.255
1°	0.204	–	0.584	0.678	0.402	0.315	0.431	–0.592	–0.110	–0.375	–0.594
2°	0.252	0.874	–	0.498	0.348	0.367	0.769	–0.334	–0.003	–0.233	–0.518
3°	0.063	0.527	0.500	–	0.904	0.237	0.574	–0.248	0.037	0.140	–0.597
4°	–0.012	0.420	0.532	0.796	–	0.327	0.531	0.029	0.124	0.325	–0.504
5°	0.062	0.218	0.306	0.516	0.699	–	0.230	0.065	0.311	–0.196	–0.498
6°	0.160	0.361	0.480	0.514	0.801	0.887	–	–0.129	0.219	0.074	–0.223
7°	–0.020	0.304	0.455	0.234	0.704	0.773	0.854	–	0.726	0.608	0.214
8°	0.045	0.585	0.657	0.291	0.617	0.643	0.655	0.845	–	0.492	–0.047
9°	–0.026	0.417	0.513	0.479	0.729	0.573	0.549	0.735	0.813	–	0.114
10°	0.053	0.530	0.557	0.787	0.900	0.687	0.779	0.689	0.597	0.770	–

Larger coefficients whose magnitude indicate significance at $\alpha = 0.05$ are in bold. For d.f. = 12, this threshold is 0.533.

It seems reasonable to assume that semiochemicals associated with the leaves, perhaps in conjunction with pheromones emitted by other beetles, in the healthy trees might contribute toward this attraction. It is also apparent that the absence of a supplemental odor attractant to the trap negatively impacted the capture of beetles in the 2014 experiments in comparison to previous experiments. Prism traps that were deployed in 2014 had capture numbers that were very similar in numbers to those recorded for the previous season in 2013 (Domingue et al., 2015). However, the branch traps only achieved a maximum capture rate of approximately 1 beetle every three days, whereas similarly traps deployed in 2013 with (Z)-3-hexen-1-ol lures had a maximum capture rate that was five times greater during the corresponding period. With the optimal foliar locations for positioning branch traps now being known, it will thus be useful to determine which odor blend might further optimize their efficacy. In addition to the (Z)-3-hexen-1-ol lures used previously in 2013, (3Z)-dodecen-12-olide pheromone might further increase attraction, as shown for other trap designs (Silk et al., 2011).

These traps have not yet been tested at low population densities for *A. planipennis*. It is encouraging that at high population densities decoy-based designs have demonstrated to be as effective as prism traps for detecting *A. planipennis* (Domingue et al., 2011, 2015). In addition, it is also not clear if the regimen of frequent clearing of the surfaces of target and non-target insects, which has been practiced in all preliminary studies (Domingue et al., 2013b, 2014, 2015), is needed to maintain a high detection rate. Concerns about preserving the fidelity of the visual signal of decoy traps is precluded in a related trap design that involves electrifying artificial decoys (Domingue et al., 2015), a feature that also eliminates the need for cumbersome Tanglefoot glue. Because such alternative decoy-based approaches operate using the same biological principles as the sticky branch traps, optimal positioning and odor baiting should be similar.

Modeling of insect dispersal through forest habitats of varying quality has been of interest in a number of systems, and has often been studied by techniques such as mark-recapture (Vairkonyi et al., 2003) and radar detection (Machial et al., 2012). Differences in dispersal rates that vary with habitat quality have been observed in such studies (Klingenberg et al., 2010). Similar studies about dispersal have been undertaken for *A. planipennis*, but because of the difficulty in developing traps for *A. planipennis* based on clearly understood behavioral principles, there have been some difficulties in fully studying the nature of their dispersal and mating behaviors. For example, based upon flight tunnel analyses, the maximum potential dispersal distances of males, virgin females, and mated females are known (Taylor et al., 2010). However, studying the dispersal and reproductive potential of females from incipient infestations to previously unaffected areas has required using labor intensive physical inspections and debarking techniques (Mercader et al., 2009; Siegert et al., 2010). It has also been noted that other aspects of adult dispersal

and mating behaviors in both sexes have been difficult to investigate empirically using such methods (Siegert et al., 2015), although attempts to model *A. planipennis* population dynamics using a number of dispersal models for females have been made (Mercader et al., 2011).

We propose that inferences about behavior and dispersal from branch traps may provide a means to obtain additional empirical data to further inform the assumptions of such models. The current study demonstrates this potential in the limited context of one heavily infested plot. For example, by using unbaited and decoy-baited branch traps and correlating captures with new and cumulative exit holes, we were also able to infer different short-range behavioral and dispersal patterns of males that correlate with local tree condition characteristics. The observation of a negative correlation of cumulative exit holes with male trap captures on decoy-baited traps late in the season when only small blocks of trees are considered, suggests that males are highly attracted to disperse from other areas to forage for mates at undamaged trees. However, the positive correlation with cumulative exit holes and decoy-baited branch traps early in the season in larger blocks, suggests that males may be foraging more broadly in areas with damaged trees early in the season. This preference may be related to factors such as greater sunlight penetration through the diminished canopy of such areas (see Vodka et al., 2009), or perhaps even a preference for odor cues from such damaged trees at that time period. Such an attraction could potentially be adaptive if females are more likely to be in these areas early in the season.

Well beyond the scope of our experiment, the low cost and ease of deployment of branch traps would also allow their use in large scale studies aimed at empirically determining a variety of parameters concerning male and female dispersal patterns. Understanding the mechanisms of *A. planipennis* dispersal is likely to be a continuing concern, even as attempts are made to quantify and predict the likely economic impacts of its spread (McCullough & Mercader, 2012), not only in the eastern North American infestation, but also elsewhere (Baranchikov et al., 2008; Straw et al., 2013; Orlova-Bienkowskaja et al., 2014.).

ACKNOWLEDGEMENTS. The work was funded by the United States Department of Agriculture, Animal and Plant Health Inspection Service program supporting the Development of Detection Tools for Exotic Buprestid Beetles (12-8130-1430-CA). S. Andreadis of Penn State University provide some assistance with the field collection of insects.

REFERENCES

- BARANCHIKOV Y., MOZOLEVSKAYA E., YURCHENKO G. & KENIS M. 2008: Occurrence of the emerald ash borer, *Agrilus planipennis* in Russia and its potential impact on European forestry. — *Bull. OEPP* **38**: 233–238.
- CAPPAERT D., MCCULLOUGH D.G., POLAND T.M. & SIEGERT N.W. 2005: Emerald ash borer in North America: a research and regulatory challenge. — *Am. Entomol.* **51**: 152–165.
- CROOK D.J., KHRIMIAN A., FRANCESE J.A., FRASER I., POLAND T.M., SAWYER A.J. & MASTRO V.C. 2008: Development of a host-based semiochemical lure for trapping emerald ash borer *Ag-*

- rilus planipennis* (Coleoptera: Buprestidae). — *Environ. Entomol.* **37**: 356–365.
- CROOK D.J., KHRIMIAN A., COSSE A., FRASER I. & MASTRO V.C. 2012: Influence of trap color and host volatiles on capture of the emerald ash borer (Coleoptera: Buprestidae). — *J. Econ. Entomol.* **105**: 429–437.
- DOMINGUE M.J., IMREI Z., LELITO J.P., MUSKOVITS J., JANIK G., CSÓKA G., MASTRO V.C. & BAKER T.C. 2013a: Field trapping of European oak buprestid beetles using visual and olfactory cues. — *Entomol. Exp. Appl.* **148**: 116–129.
- DOMINGUE M.J., LELITO J.P., FRASER I., MASTRO V.C., TUMLINSON J.H. & BAKER T.C. 2013b: Visual and chemical cues affecting the detection rate of the emerald ash borer in sticky traps. — *J. Appl. Entomol.* **137**: 77–87.
- DOMINGUE M.J., LAKHTAKIA A., PULSIFER D.P., HALL L.P., BADDING J.V., BISCHOF J.L., MARTÍN-PALMA R.J., IMREI Z., JANIK G. ET AL. 2014: Bioreplicated visual features of nanofabricated buprestid beetle decoys evoke stereotypical male mating flights. — *Proc. Natn. Acad. Sci. U.S.A.* **111**: 14106–14111.
- DOMINGUE M.J., PULSIFER D.P., LAKHTAKIA A., BERKEBILE J., STEINER K.C., LELITO J.P., HALL L.P. & BAKER T.C. 2015: Detecting emerald ash borers (*Agrilus planipennis*) using branch traps baited with 3D-printed beetle decoys. — *J. Pest Sci.* **88**: 267–279.
- FRANCESE J.A., MASTRO V.C., OLIVER J.B., LANCE D.R., YOUSSEF N. & LAVALLEE S.G. 2005: Evaluation of colors for trapping *Agrilus planipennis* (Coleoptera: Buprestidae). — *J. Entomol. Sci.* **40**: 93–95.
- FRANCESE J.A., OLIVER J.B., FRASER I., LANCE D.R., YOUSSEF N., SAWYER A.J. & MASTRO V.C. 2008: Influence of trap placement and design on capture of the emerald ash borer (Coleoptera: Buprestidae). — *J. Econ. Entomol.* **101**: 1831–1837.
- FRANCESE J.A., CROOK D.J., FRASER I., LANCE D.R., SAWYER A.J. & MASTRO V.C. 2010a: Optimization of trap color for emerald ash borer (Coleoptera: Buprestidae). — *J. Econ. Entomol.* **103**: 1235–1241.
- FRANCESE J.A., FRASER I., RIETZ M.L., CROOK D.J., LANCE D.R. & MASTRO V.C. 2010b: Relation of prism trap color, size and canopy placement in determining capture of emerald ash borer (Coleoptera: Buprestidae). — *Can. Entomol.* **142**: 596–600.
- FRANCESE J.A., FRASER I., LANCE D.R. & MASTRO V.C. 2011: Efficacy of multifunnel traps for capturing emerald ash borer (Coleoptera: Buprestidae): Effect of color, glue, and other trap coatings. — *J. Econ. Entomol.* **104**: 901–908.
- FRANCESE J.A., RIETZ M.L., CROOK D.J., FRASER I., LANCE D.R. & MASTRO V.C. 2013: Improving detection tools for the emerald ash borer (Coleoptera: Buprestidae): Comparison of prism and multifunnel traps at varying population densities. — *J. Econ. Entomol.* **106**: 2407–2414.
- GRANT G.G., RYALL K.L., LYONS D.B. & ABOU-ZAID M.M. 2010: Differential response of male and female emerald ash borers (Col., Buprestidae) to (Z)-3-hexenol and manuka oil. — *J. Appl. Entomol.* **134**: 26–33.
- HAACK R.A., JENDEK E., LIU H., MARCHANT K.R., PETRICE T.R., POLAND T.M. & YE H. 2002: The emerald ash borer: A new exotic pest in North America. — *Newsl. Mich. Entomol. Soc.* **47**: 1–5.
- HAAVIK L., COLEMAN T.W., FLINT M.L., VENETTE R.C. & SEYBOLD S.J. 2012: *Agrilus auroguttatus* exit hole distributions on *Quercus agrifolia* boles and a sampling method to estimate their density on individual trees. — *Can. Entomol.* **144**: 1–12.
- KLINGENBERG M.D., BJÖRKLUND N. & AUKEMA B.H. 2010: Seeing the forest through the trees: differential dispersal of *Hylobius warreni* wood within modified forest habitats. — *Environ. Entomol.* **39**: 898–906.
- LELITO J.P., FRASER I., MASTRO V.C., TUMLINSON J.H., BÖRÖCZKY K. & BAKER T.C. 2007: Visually mediated ‘paratrooper copulations’ in the mating behavior of *Agrilus planipennis* (Coleoptera: Buprestidae), a highly destructive invasive pest of North American ash trees. — *J. Insect Behav.* **20**: 537–552.
- LELITO J.P., FRASER I., MASTRO V.C., TUMLINSON J.H. & BAKER T.C. 2008: Novel visual-cue-based sticky traps for monitoring of emerald ash borers, *Agrilus planipennis* (Coleoptera: Buprestidae). — *J. Appl. Entomol.* **132**: 668–674.
- MACHIAL L.A., LINDGREN B.S., STEENWEG R.W. & AUKEMA B.H. 2012: Dispersal of Warren root collar weevils (Coleoptera: Curculionidae) in three types of habitat. — *Environ. Entomol.* **41**: 578–586.
- MARSHALL J.M., STORER A.J., FRASER I. & MASTRO V.C. 2010: Efficacy of trap and lure types for detection of *Agrilus planipennis* (Coleoptera: Buprestidae) at low density. — *J. Appl. Entomol.* **134**: 296–302.
- MCCULLAGH P. & NELDER J.A. 1989: *Generalized Linear Models*. 2nd ed. Chapman & Hall, London, 532 pp.
- MCCULLOUGH D.G. & MERCADER R.J. 2012: Evaluation of potential strategies to SLOW Ash Mortality (SLAM) caused by emerald ash borer (*Agrilus planipennis*): SLAM in an urban forest. — *Int. J. Pest Manag.* **58**: 9–23.
- MERCADER R.J., SIEGERT N.W., LIEBHOLD A.M. & MCCULLOUGH D.G. 2009: Dispersal of the emerald ash borer, *Agrilus planipennis*, in newly-colonized sites. — *Agr. For. Entomol.* **11**: 421–424.
- MERCADER R.J., SIEGERT N.W., LIEBHOLD A.M. & MCCULLOUGH D.G. 2011: Influence of foraging behavior and host spatial distribution on the localized spread of the emerald ash borer, *Agrilus planipennis*. — *Popul. Ecol.* **53**: 271–285.
- ORLOVA-BIENKOWSKAJA & MARINA J. 2014: Ashes in Europe are in danger: the invasive range of *Agrilus planipennis* in European Russia is expanding. — *Biol. Invas.* **16**: 1345–1349.
- POLAND T.M. & MCCULLOUGH D.G. 2014: Comparison of trap types and colors for capturing emerald ash borer adults at different population densities. — *Environ. Entomol.* **43**: 157–170.
- RYALL K., SILK P.J., FIDGEN J., MAYO P., LAVALLÉE R., GUERTIN C. & SCARR T. 2015: Effects of pheromone release rate and trap placement on trapping of *Agrilus planipennis* (Coleoptera: Buprestidae) in Canada. — *Environ. Entomol.* **40**: 734–745.
- SIEGERT N.W., MCCULLOUGH D.G., WILLIAMS D.W., FRASER I., POLAND T.M. & PIERCE S.J. 2010: Dispersal of *Agrilus planipennis* (Coleoptera: Buprestidae) from discrete epicenters in two outlier sites. — *Environ. Entomol.* **39**: 253–265.
- SIEGERT N.W., MERCADER R.M. & MCCULLOUGH D.G. 2015: Spread and dispersal of emerald ash borer (Coleoptera: Buprestidae): estimating the spatial dynamics of a difficult-to-detect invasive forest pest. — *Can. Entomol.* **147**: 338–348.
- SILK P.J., RYALL K., MAYO P., LEMAY M.A., GRANT G., CROOK D., COSSÉ A., FRASER I., SWEENEY J.D., LYONS D.B., PITT D., SCARR T. & MAGEE D. 2011: Evidence for a volatile pheromone in *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) that increases attraction to a host foliar volatile. — *Environ. Entomol.* **40**: 904–916.
- STEINER K.C., WILLIAMS M.W., DEHAYES D.H., HALL R.B., ECKERT R.T., BAGLEY W.T., LEMMIEN W.A., KARNOSKY D.F., CARTER K.K. & CEC H.F.C. 1988: Juvenile performance in a range-wide provenance test of *Fraxinus pennsylvanica* Marsh. — *Silvae Genet.* **37**: 104–111.
- STRAW N.A., WILLIAMS D.T., KULINICH O. & GNINENKO Y.I. 2013: Distribution, impact and rate of spread of emerald ash borer *Agrilus planipennis* (Coleoptera: Buprestidae) in the Moscow region of Russia. — *Forestry* **86**: 515–522.

- TAYLOR R.A.J., BAUER L.S., POLAND T.M. & WINDELL K.N. 2010: Flight performance of *Agrilus planipennis* (Coleoptera: Buprestidae) on a flight mill and in free flight. — *J. Insect Behav.* **23**: 128–148.
- VARKONYI G., KUUSSAARI M. & LAPPALAINEN H. 2003: Use of forest corridors by boreal *Xestia* moths. — *Oecologia* **137**: 466–474.
- VODKA S., KONVICKA M. & CIZEK L. 2009: Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. — *J. Insect Conserv.* **13**: 553–562.

Received April 3, 2016; revised and accepted July 25, 2016
Published online August 25, 2016