M.L. 2013, Chp. 52, Sec. 2, Subd. 06cB & M.L. 2016, Chapter 186, Section 2, Subdivision 18

Project Abstract
For the Period Ending June 30, 2017

PROJECT TITLE:	Improving Emerald Ash Borer Detection Efficacy for Control – Part B
PROJECT MANAGER:	Brian Aukema
AFFILIATION:	University of Minnesota
MAILING ADDRESS:	1980 Folwell Avenue
CITY/STATE/ZIP:	St Paul, MN 55108
PHONE:	(612) 625-5299
E-MAIL:	BrianAukema@umn.edu
WEBSITE:	http://www.forest-insects.umn.edu
FUNDING SOURCE:	Environment and Natural Resources Trust Fund
LEGAL CITATION:	M.L. 2013, Chp. 52, Sec. 2, Subd. 06cB & M.L. 2016, Chp 186, Sec. 2, Subd. 18

APPROPRIATION AMOUNT:	$ 360,000
AMOUNT SPENT:	$ 358,125
AMOUNT REMAINING:	$ 1,875

Overall Project Outcomes and Results

The emerald ash borer is an extremely challenging insect to manage because (1) there is a long lag phase between initial infestation and tree decline/mortality and (2) the insect is difficult to monitor and detect. There are several detection tools available, such as laboriously peeling the bark from branches harvested from trees, visual inspection of trees for evidence of woodpecker feeding, and attraction to purple prism traps hung in ash trees during periods of adult flight. We calibrated these detection tools to provide an estimate of the efficacy of these tools across different population densities of emerald ash borer. We found that visual evaluations to monitor trees for woodpecker damage are an effective method for identifying EAB at low densities prior to wide-spread tree decline. We found that 50 to 78% of trees at an infestation site will show signs of woodpecker damage before larval densities are high enough to cause irreparable damage to the tree. Visual inspections during leaf-off conditions are more inexpensive than other methods, and can be used by local communities to detect and respond to populations early.

We were able to use these project funds to leverage a federal grant to investigate the impact of strategic and targeted tree removals if emerald ash borer is detected early in a community. We published a scientific paper (Fahrner, Abrahamson, Venette, and Aukema 2017 “Strategic removal of host trees in isolated, satellite infestations of emerald ash borer can reduce population growth” Urban Forestry & Urban Greening 24:184-194) that found that removal of two thirds of the trees in the Twin Cities area where EAB was first detected in 2009 reduced populations by just over one half over the course of five years. These strategic removals slowed population growth considerably, and set populations back by at least one year. The most significant impact was achieved by targeting trees with evidence of woodpecker feeding.

Finally, studying potential tradeoffs between Minnesota’s colder climate (than other places in emerald ash borer’s range) and dispersal capacity, we found that overwintering location affects survival rates, but not energy reserves or flight capacity. In other words, Minnesota might be cold, but surviving insects do not appear to be less capable of dispersing in the spring.

Project Results Use and Dissemination

This was a joint partnership with the Minnesota Department of Agriculture. The primary audience for this work was disseminated to municipalities and other entities responsible for managing EAB at the local level.

Information was conveyed through meetings held throughout the year, both at MDA through the EAB Forum (bimonthly meeting) and also through conferences, meetings and workshops held around the state and also at professional and technical conferences.

Environment and Natural Resources Trust Fund (ENRTF) M.L. 2013 Work Plan Final Report

Date of Final Report:	Oct 25, 2017	
Final Report		
Date of Work Plan Approval:	June 11, 2013	
Project Completion Date:	June 30, 2017	**Is this an amendment request?** Yes

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PROJECT TITLE: Improving Emerald Ash Borer Detection Efficacy for Control – Part B

Project Manager: Brian Aukema
Affiliation: University of Minnesota
Mailing Address: 1980 Folwell Avenue
City/State/Zip Code: St Paul, MN 55108
Telephone Number: (612) 625-5299
Email Address: BrianAukema@umn.edu
Web Address:

Location: Region: Statewide, Metro, Southeast
Counties: Statewide, Hennepin, Houston, Ramsey, Winona

Total ENRTF Project Budget:

ENRTF Appropriation:	**$360,000**
Amount Spent:	**$358,116**
Balance:	**$1,884**

Legal Citation: M.L. 2013, Chp. 52, Sec. 2, Subd. 06cB
M.L. 2016, Chapter 186, Section 2, Subdivision 18

Appropriation Language:
$600,000 the first year is from the trust fund to evaluate and implement options for effective detection of the presence of emerald ash borer. Of this appropriation, $240,000 is to the commissioner of agriculture and $360,000 is to the Board of Regents of the University of Minnesota. This appropriation is available until June 30, 2016, by which time the project must be completed and final products delivered.

Carryforward: (a) The availability of the appropriations for the following projects are extended to June 30, 2017: (6) Laws 2013, chapter 52, section 2, subdivision 6, paragraph (c), Improving Emerald Ash Borer Detection Efficacy for Control.

I. PROJECT TITLE: Improving Emerald Ash Borer Detection Efficacy for Control – Part B, U of M

II. PROJECT STATEMENT:

Emerald ash borer (EAB) was first discovered in Minnesota in 2009 in St Paul. It is now known to occur in four Minnesota Counties (Ramsey, Hennepin, Houston and Winona) as of September, 2012. Minnesota has more ash than any other area of the U.S. and ash is an important component of our rural and urban forests. Much work has been done to stem the spread of EAB throughout Minnesota including education, quarantine, detection surveys and biological control efforts. The likely consequence of taking no action against EAB is its rapid spread through most of the state and the resulting death of > 99% of the ash trees in those areas.

Detection is a key obstacle to controlling EAB. Minnesota has worked with the United State Department of Agriculture (USDA) to conduct detection surveys for EAB since 2003 using a variety of techniques – most recently large, purple traps. However, EAB detection tools have not been calibrated to provide an estimate of what population density of EAB they are able to detect. This is a critical information gap as EAB population density is a critical parameter in determining how and where to implement control measures.

This project will evaluate a range of detection tools and measure their ability to detect EAB at different population densities. We will also evaluate aspects of EAB biology that are critical in estimating dispersal and consequently, spread. We will use different detection techniques in and around EAB-infested areas in order to compare their ability to detect EAB. We will work with local governments to implement this work.

Through this project we will gain a better understanding as to the feasibility of using EAB detection surveys to inform EAB management for local governments or others.

III. PROJECT STATUS UPDATES:

Project Status as of November 15, 2013**:**
This project is off to a good start and on track with work goals and planned spending. Work has been initiated for both activities and is on schedule with targeted outcomes. No problems have been encountered to date that will delay or change the planned schedule of work. Specific details on work accomplished to date are provided under each of the activity sections below.

Project Status as of May 15, 2014**:**
No changes to report. Project is on track. See specific activities.

Project Status as of November 15, 2014**:** This project continues to go well. Winter mortality to emerald ash borer was surprisingly high such that low density populations – the most critical knowledge gap in sampling – have not grown as fast as initially expected. The MDA continues to collect data that will be analyzed as populations grow. One key question is the effect that early management intervention may have once low density populations are detected. We were able to successfully leverage this LCCMR on monitoring of EAB to a federal agency (USDA APHIS) for a $35,000 grant to study the efficacy of sanitation on the population growth of EAB once low density, satellite infestations of EAB are detected. For the current project, no problems have been encountered that will delay or change the planned schedule or scope of work. Specific details on work accomplished to date are provided under each of the activity sections below.

Project Status as of May 15, 2015**:** Project is proceeding as planned. Last year at this time we were most concerned about the lack of high density populations of EAB due to winter mortality, as it is important to develop these monitoring methods across a range of densities. However our fears were (unfortunately) alleviated with the expected rise in populations in four sites over the past year. The MDA report details our site replacement plans. A graduate student was recruited to work on Activity 2

Project Status as of November 15, 2015**:** Project is making very good progress. As noted in the MDA report, we are seeing increasing populations of EAB across the state, with several new finds. This project led to the first confirmed find in Duluth in a low-density infestation using branch sampling. Activity 2 (tradeoff between lipid content and dispersal) continues in full gear, although the delay in finding a suitable student until Jan 2015 necessitates a request for a no-cost extension to finish that activity (see below). Initial experiments were completed during the winter of 2014-2015. Preliminary results were analyzed, summarized, and presented at a regional professional conference.

Amendment Request (Nov 24, 2015): We are requesting a one year extension to this project to June 30, 2017 with no changes to budget or scope of work. Master's student Mr. Dylan Tussey was recruited to the project in January 2015 (18 months after project initiation). This extension will allow him to complete his thesis requirements. **[Ammendment Approved 12-08-15].**

Project Status as of May 15, 2016**:** Project continues to make good progress. (As, well, there have been several new finds of EAB in the past six months, as the insect continues to spread). The MDA completed plot sampling in the fall with a data exchange to the UMN team this spring. Activity 1 displays the start of spatial analysis of one of the sampling designs of one of the plots. In Activity 2, insects have been reared from logs that have overwintered in two climatically-distinct locations. These insects are now being analyzed on the flight mill as well as being subjected to physiological assays measuring lipid content. Results from the last progress report were presented at a national meeting in November.

Project Status as of Nov 15, 2016**:** All field data have been collected and passed from the MDA to the U. The next six months will look a lot like the past six months: data analysis. We reported on some spatial analysis in Activity 1 in the last progress report; we are finding, however, that there are few spatial relationships at the plot level scales that were collected. This is not an unexpected result; it simply reflects the biology of the insect. If a tree starts showing symptoms of emerald ash borer infestation, it is likely that all the trees in the 100m vicinity will show symptoms. In many ways, this simplifies data analysis in the next six months as we move toward finding the best sampling method at a given emerald ash borer density. In Activity 2, additional insects have been subjected to physiological assays measuring lipid content. Results were presented by the graduate student at two conferences.

Retroactive Amendment Request 10/25/17

In Activity 1, we ended with $1684 cost savings accumulated in *travel* (able to use lab vehicle for periods instead of exclusive UMN Fleet rental) and *other/publications* (published scientific article in journal without page charges). We request to redistribute this $1684 amount to *personnel*. We engaged our senior lab technician Aubree Kees at times to help the graduate student, as she had experience scouting emerald ash borer prior to coming to the University of Minnesota. That portion of graduate student time was moved to a federal project leveraged with LCCMR funds; the small overage in salary is due to differences in benefits rates.
In Activity 2, we ended with $1904 savings in *supplie*s (did not need to replace many temperature sensors), $3,389 in travel (combined travel with Activity 1 whenever possible and EAB populations remained close to metro area through life of project), and $1,000 in publications (Ent Soc of America unexpectedly dropped page charge fees from their journals). These amounts total $6,293. We request to redistribute $4,409 of these savings to personnel; a postdoctoral scholar with international expertise in dispersal of invasive species assisted with project completion as the graduate student completed his degree. These changes leave a balance of $1,884 unspent that we return to the ENRTF with project completed.

Overall Project Outcomes and Results

The emerald ash borer is an extremely challenging insect to manage because (1) there is a long lag phase between initial infestation and tree decline/mortality and (2) the insect is difficult to monitor and detect. There are several detection tools available, such as laboriously peeling the bark from branches harvested from trees, visual inspection of trees for evidence of woodpecker feeding, and attraction to purple prism traps hung in ash trees during periods of adult flight. We calibrated these detection tools to provide an estimate of the efficacy of these tools across different population densities of emerald ash borer. We found that visual evaluations to monitor trees for woodpecking damage are an effective method for identifying EAB at low densities prior to wide-spread tree decline. We found that 50 to 78% of trees at an infestation site will show signs of woodpecking damage before larval densities are high enough to cause irreparable damage to the tree. Visual inspections during leaf-off conditions are more inexpensive than other methods, and can be used by local communities to detect and respond to populations early.

We were able to use these project funds to leverage a federal grant to investigate the impact of strategic and targeted tree removals *if emerald ash borer is detected early in a community*. We published a scientific paper (Fahrner, Abrahamson, Venette, and Aukema 2017 "Strategic removal of host trees in isolated, satellite infestations of emerald ash borer can reduce population growth" Urban Forestry & Urban Greening 24:184-194) that found that removal of two thirds of the trees in the Twin Cities area where EAB was first detected in 2009 reduced populations by just over one half over the course of five years. These strategic removals slowed population growth considerably, and set populations back by at least one year. The most significant impact was achieved by targeting trees with evidence of woodpecker feeding.

Final, studying potential tradeoffs between Minnesota's colder climate (than other places in emerald ash borer's range) and dispersal capacity, we found that overwintering location affects survival rates, but not energy reserves or flight capacity. In other words, Minnesota might be cold, but surviving insects do not appear to be less capable of dispersing in the spring.

IV. PROJECT ACTIVITIES AND OUTCOMES:

ACTIVITY 1: Implement detection surveys for EAB to evaluate efficacy of different detection techniques under different abundances of EAB

Description:
We will conduct detection surveys for EAB in and around infested areas. The purpose of working in these areas will be to measure the efficacy of different detection techniques. The techniques will include visual evaluation (low labor input), purple traps and / or EAB cadaver traps (moderate labor input) and removal and sampling tree branches (high labor input). We will also visually evaluate tree canopy and stem condition in these areas so as to relate the results of the detection work to tree health. We will gather data from trees felled by cooperators for EAB sanitation when possible to estimate EAB population density in these areas. This is a labor intensive task, but important to understanding the efficacy of the detection techniques (i.e., at what population density are they detecting EAB?).

MDA - Part A
This work will be coordinated by MDA who will hire one temporary employee for this task. The employee is anticipated to spend 80% of their time on this project. In addition, MDA staff funded by other EAB projects will collect information that will contribute to this project as well.

UMN - Part B
Sampling design and analysis will be coordinated by Drs. Aukema and Venette. One graduate student and one undergraduate student advised by Dr. Aukema will also work on sampling design and analysis as well as data collection. All sampling work will be coordinated by MDA with local government cooperators who will also assist by felling branches for sampling.

Summary Budget Information for Activity 1, UMN - Part B:	**ENRTF Budget:**	**$ 210,750**
	Amount Spent:	**$ 210,750**
	Balance:	**$ 0**

Activity Completion Date:

Outcome	**Completion Date**	**Budget**
1. Year 1 - Visual assessment of canopy condition in detection areas, associated data management and analysis	September 2013	$ 28,725 (UMN)
2. Year 1 **-** Branch and tree sampling in detection areas, visual assessment of stem condition, associated data management and analysis	April 2014	$ 30,908 (UMN)
3. Year 2 - Trap survey for EAB in detection areas, visual assessment of canopy condition, associated data management and analysis	September 2014	$ 39,008 (UMN)
4. Year 2 - Branch and tree sampling in detection areas, visual assessment of stem condition, associated data management and analysis	April 2015	$ 31,408 (UMN)
5. Year 3 - Trap survey for EAB in detection areas, visual assessment of canopy condition, associated data management and analysis	September 2015	$ 39,008 (UMN)
6. Year 3 - Branch and tree sampling in detection areas, visual assessment of stem condition, associated data management and analysis	April 2015	$ 31,408 (UMN)
7. Develop, print and distribute informational materials related to project	June 2016	$ 10,283 (UMN)

Activity Status as of November 15, 2013**:**

UMN

Data analysis has not yet commenced as the project has just begun. Activities have been restricted to advertising and hiring a technician to work on this part of the project. As part of onboarding process, the technician underwent training of crown ratings of infested ash in the Minneapolis/Seward neighborhoods. Training has gone well, as the candidate had prior experience with tree inventory work in preparation of emerald ash borer in another state prior to relocation to the University of Minnesota to join this project.

See MDA Project Report for description of progress for MDA work.

Activity Status as of May 15, 2014**:**

We designed a sampling plan with our MDA collaborators (see MDA report). The MDA has been taking a lead role in field data collections and detection surveys. Other than some data curation, the technician was temporarily assigned to another project as the bulk of this work will take place in the latter half of the project as we analyze sampling methods and detection efficacy as the infestation progresses.

See MDA Project Report for description of progress for MDA work.

Activity Status as of November 15, 2014**:** The majority of analysis will occur in the latter parts of the project once we have gathered as much data as possible. We were able to leverage this project for a federal grant to study the effects of early and aggressive management of EAB in satellite infestations in locations isolated from major influxes of surrounding beetles. This work integrates well with this project’s focus on determining the best sampling methods for detecting low density populations of emerald ash borer. Two presentations were given that highlighted this work (see dissemination below), including one at the Upper Midwest Invasive Species Conference in Duluth in October. Another has been invited at the national Entomological Society of America (meeting next week) as LCCMR’s investment in monitoring, detection, and development and implementation of biological control for emerald ash borer continues to garner national attention in the forest health community. (Project funds are not being used to travel out-of-state).

See MDA Project Report for description of progress for MDA work.

Activity Status as of May 15, 2015: The MDA report summarizes results of visual and branch sampling methods to date. We are now beginning to see the range of densities needed for good statistical "calibration" of these sampling techniques, with between 0-75 larvae per square meter. We have met to determine replacement strategies for the increasing numbers of trees being removed due to mortality. On the modeling side we have begun implementing some of these early techniques (e.g., wood-pecking) with the federal grant leveraged above to determine *which* trees provide the best population-wide management if removed when appropriately detected. We are trying to determine if the effort to remove woodpecked trees, for example, is worth the investment in finding them, and if so, how much time might it buy?

See MDA Project Report for description of progress for MDA work.

Activity Status as of November 15, 2015: We continue work on modeling removal of early-detected trees in concert with the federal grant that was leveraged to quantify the delay in population expansion from removing infested trees. A focus has been to estimate the number of emerald ash borer larvae on the landscape. We have been focusing on the region of the core infested area of the Twin Cities from 2009-present to estimate a scenario *without* any management intervention (Fig. 1). This is useful to determine in future steps how many ash borers may have been/will be removed once trees were/are a) detected and b) removed at different time steps in the inevitable population increase.

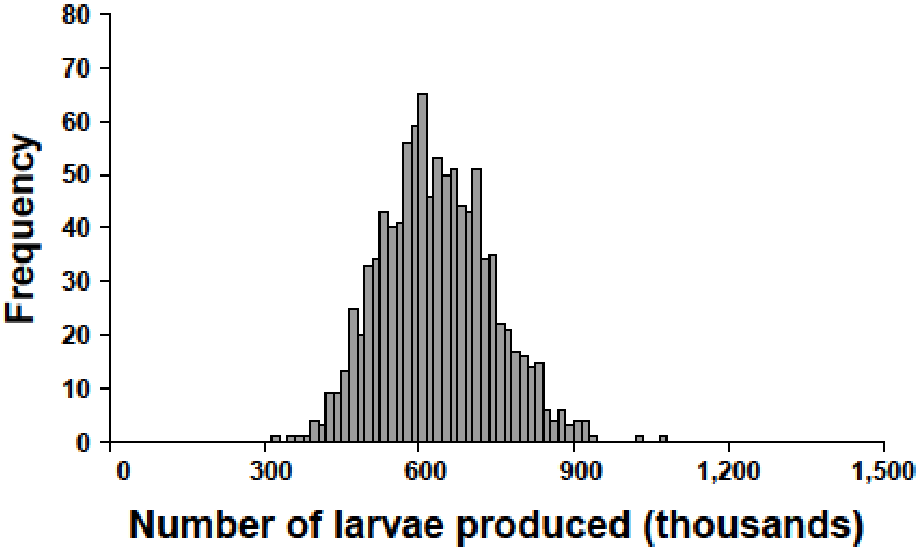
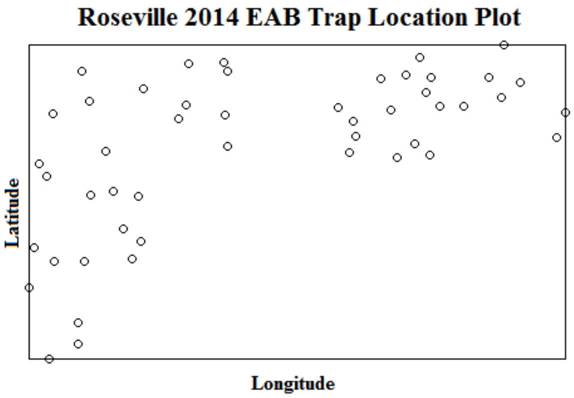


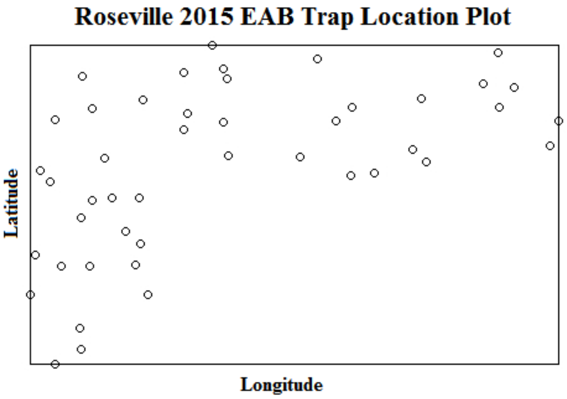
Fig. 1: Estimate of number of emerald ash borers that would have been produced 2009-2014 without any management activities, Twin Cities, MN

Initial estimates (above) indicate that just in the core area of the metro, there would have been upwards of 600,000 insects by now if no management activities had taken place. Our initial estimates of numbers of insects removed by management (once detected) indicate that sanitation may be effective if performed in isolation from other infested area, but the delay in population growth may not last more than 4 years. Nevertheless, this may buy cities or municipalities valuable time to formulate other long term control strategies. We have drafted a manuscript that will be submitted to a peer-reviewed journal during the next period. Work will also continue on analysis of best detection methods at different EAB densities from the field data once the winter data is collected from our MDA partners.

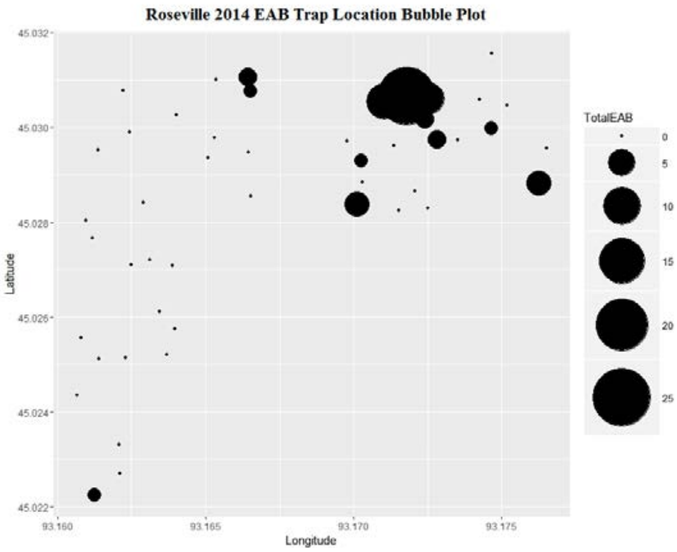
Activity Status as of May 15, 2016:

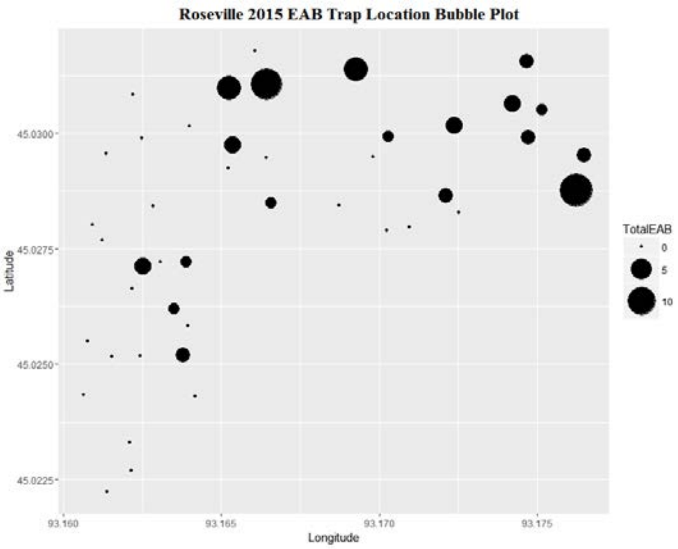
The emerald ash borer (EAB) detection data package from 2013-2016 gathered by our MDA friends was received this spring. Data is currently being process and analyzed. These data include branch sampling, trap catches, visual assessment of EAB damage, gallery sampling and whole tree sampling from 2013-2016 from multiple sites in Minnesota, ranging from Duluth to Great River Bluffs State Park, and several sites in the metro area including Fort Snelling, Roseville and others.
Spatial analysis is being used to compare the efficacy of sampling techniques at each site, over multiple years. For example, the graphs below show the spatial distribution of the EAB traps used in 2014 and 2015 at the Roseville study site.



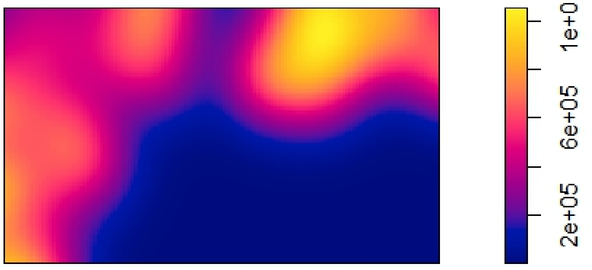


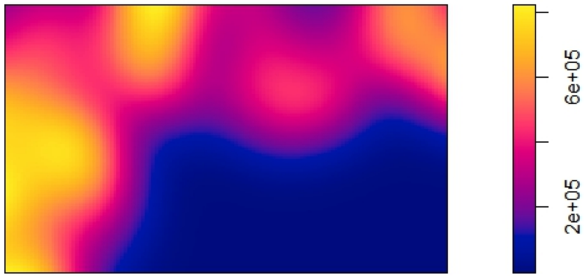
We use bubble plots, below, to view the spatial point pattern of EAB trap captures for each trap in the study area. The circle radii represent the total number of EAB captured in each trap throughout the given year. Here we can see differences in the quantity of total EAB caught and the location of trap catches from one year to another.

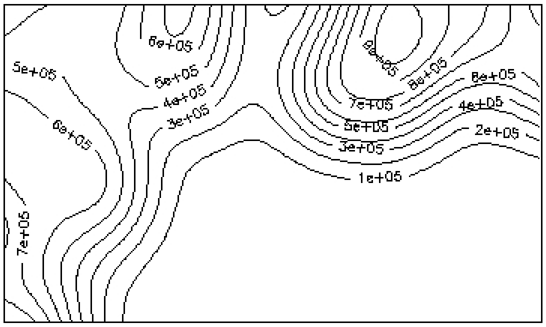


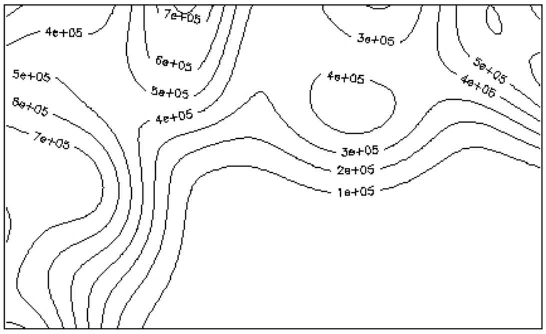


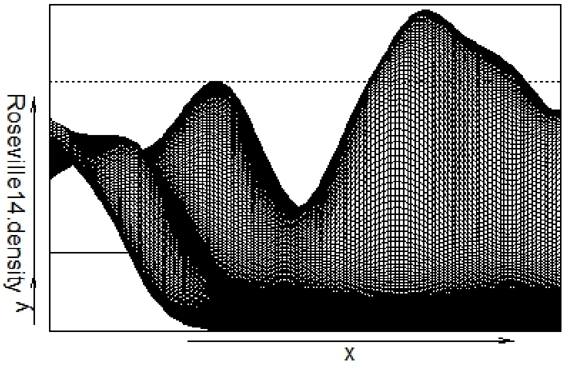
Spatial point process analysis is being used to depict the spatial density of the total number of EAB caught in traps throughout the year in 2014 and 2015 at the Roseville study site. The response variable has been rescaled for analytical reasons, but this provides the reader an illustration of some of the techniques being used (next page).

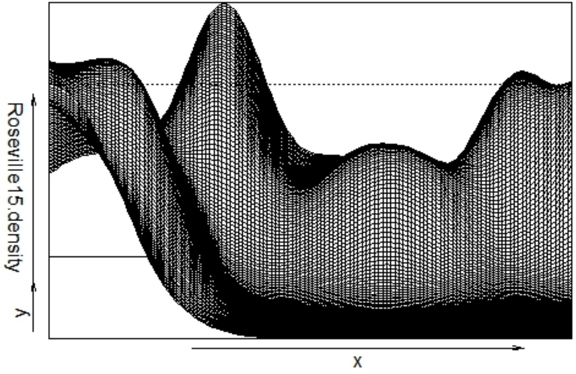

Roseville 2014 EAB Trap Catch Plot


Roseville 2015 EAB Trap Catch Plot


Roseville 2014 EAB Trap Catch Contour


Roseville 2015 EAB Trap Catch Contour


Roseville 2014 EAB Trap Catch Density

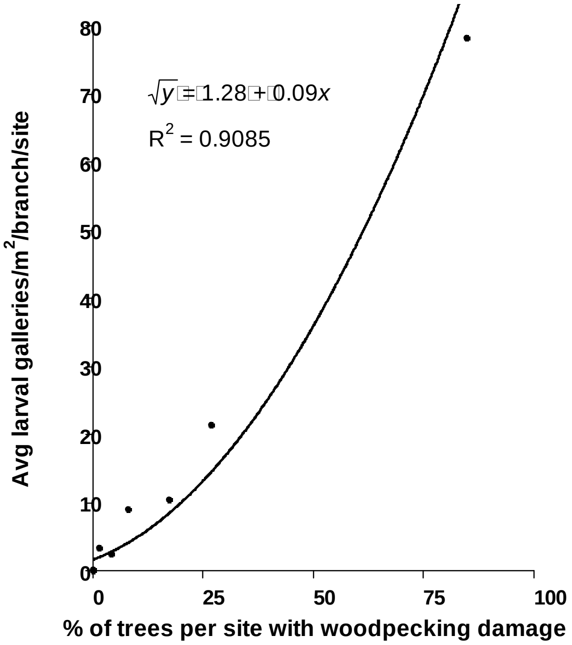

Roseville 2015 EAB Trap Catch Density

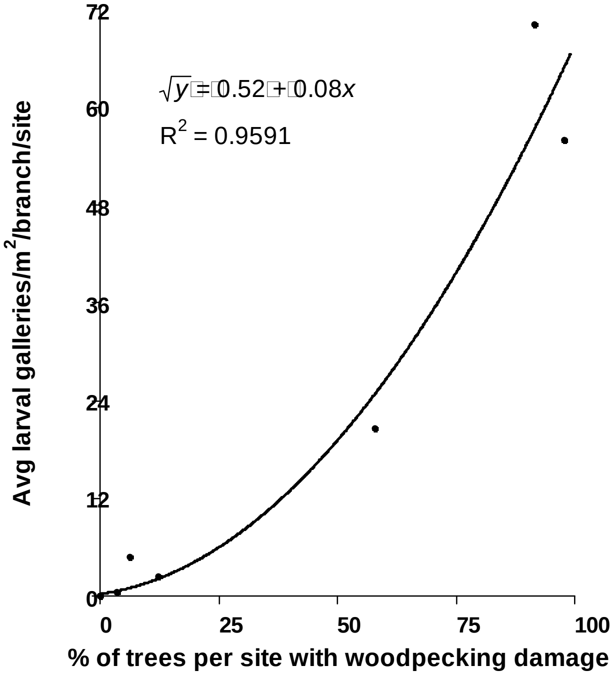
From these steps of interpolating surfaces we can move into further quantitative analyses.

Activity Status as of November 15, 2016:

We continue to analyze data on the relationships between branch sampling, trap catches, visual assessment of EAB damage, gallery sampling and whole tree sampling from 2013-2016 from multiple sites in Minnesota, ranging from Duluth to Great River Bluffs State Park, and several sites in the metro area including Fort Snelling, Roseville and others. The data from 2013-2014 is behaving better than the 2015 data.
We include two graphs below to show the relationship between woodpecking damage and the average number of galleries of EAB larvae in a tree. Canopy dieback typically becomes apparent once densities reach approximately 25 insects per square yard of phloem.

2013 2014

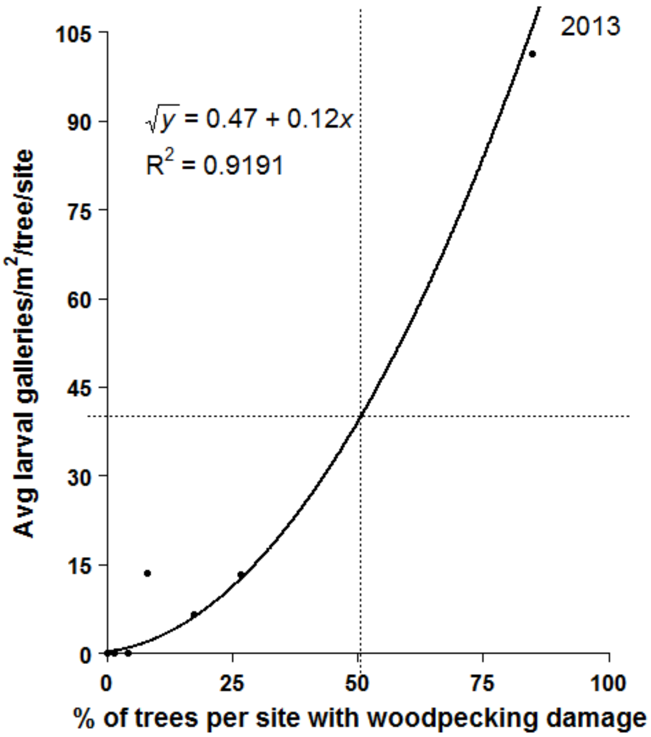


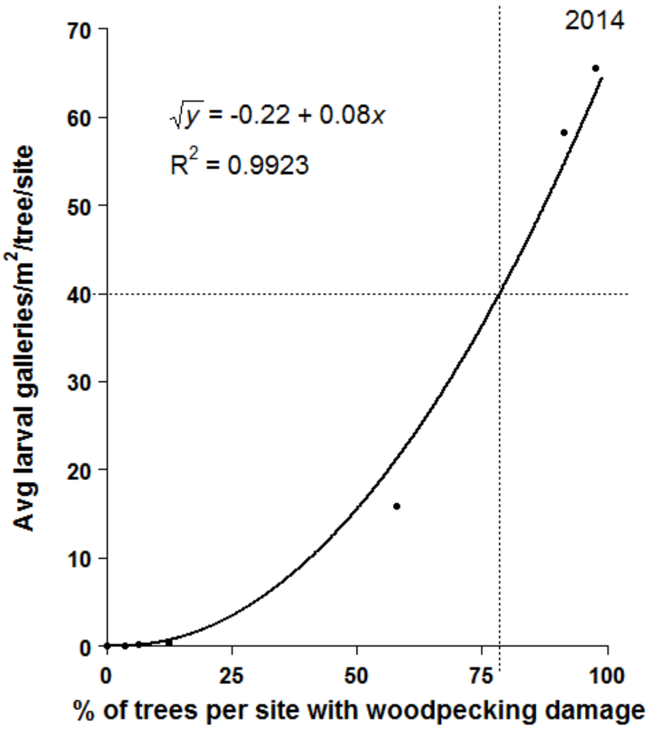


We are extending these site-level regression analyses to other measures of EAB population density such as EAB trap catches.

Final Report Summary:

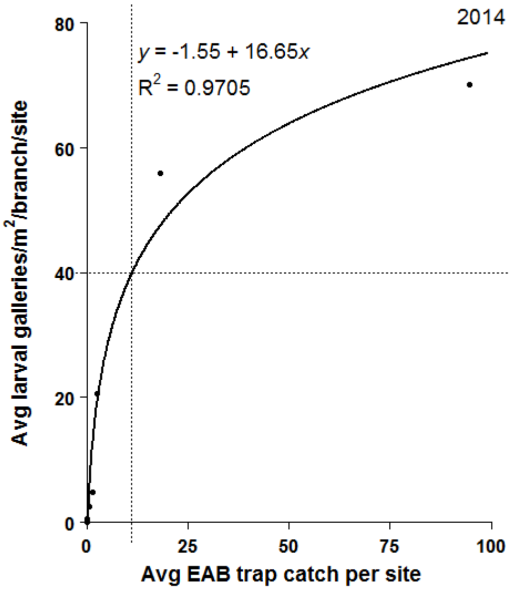
We found that visual inspection of woodpecking damage was the best method of detecting low density infestations of EAB. In the final phase of the project, we correlated woodpecking damage with the average number of larval galleries in the whole tree (an extension of branch sampling, see above). We were pleased that the relationships remained quite strong (see next page).





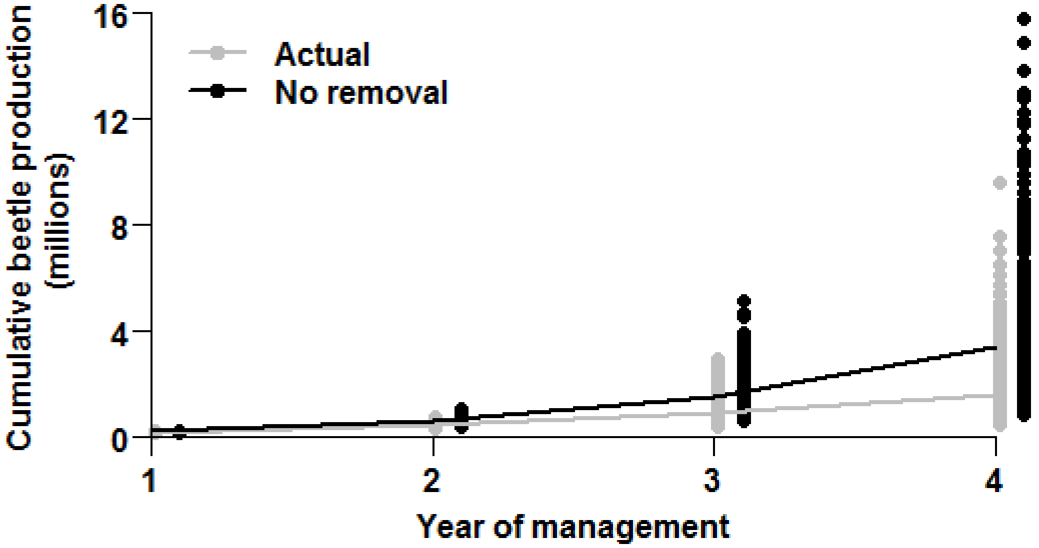
The cross hatching on the figure shows where 50% percent (2013) and 76% (2014) of trees surveyed with evidence of woodpecker feeding intersect with an average density of 40 galleries of emerald ash borer larvae per square meter of bark surface. Forty larvae per square meter is recognized as the point above where a tree may no longer be treatable, and death becomes inevitable.

For comparison, we include a graph of the 2014 data of purple prism catches on the next page. The graph shows that once as few as 10 adult EAB are captured in the traps, the surrounding trees are already likely to be well-infested and untreatable. Based on the eight sites, this sampling technique is precise (i.e., the line fits very well) but primarily indicates that if traps are catching EAB in high numbers, most of the surrounding trees are already heavily infested.



We found that these relationships broke down in 2015 as populations in some of the high density sites became too high.

Using federal funds, we were able to estimate the impact of tree removal on growth rates of the insect in the Twin Cities metro area. We were excited to prove that removal of two thirds of the trees in the Twin Cities area where EAB was first detected in 2009 reduced populations by just over one half over the course of five years. These strategic removals slowed population growth considerably, and set populations back by at least one year. The most significant impact was achieved by targeting trees with evidence of woodpecker feeding. Below we reproduce one graph from the paper.



Caption: Cumulative beetle production under *actual* versus *no removal* scenarios across four years (2010-2013) of management in Minneapolis-Saint Paul, MN, USA

This work was published in Fahrner, Abrahamson, Venette, and Aukema 2017 “Strategic removal of host trees in isolated, satellite infestations of emerald ash borer can reduce population growth” Urban Forestry & Urban Greening 24:184-194.

ACTIVITY 2: Implement field and laboratory experiments to examine factors affecting dispersal distances and winter survival of EAB.

Description:
We will measure the effect of winter cold on dispersal by measuring the fat content of beetles held under different temperature regimes. It is possible that beetles held at lower temperatures will have lower lipid reserves and therefore shorter dispersal ability. This is an important consideration when predicting spread rates of EAB in different areas of the state. We will also model the relationship between air temperature and the temperature within trees where EAB overwinter. This is a critical gap in our understanding of the impact of winter on EAB. This work will be conducted by Dr. Venette, one graduate student and one undergraduate assistant. Initial work on the overwintering biology of EAB is being completed by Dr. Venette as a result of the ENRTF project "Ecological and Hydrological Impacts of Emerald Ash Borer" which was initiated in July 2010. That work investigated the effect of host (green ash vs black ash) on the supercooling point and lower lethal temperature of EAB. The proposed project would take the next step to investigate the impact of non-lethal cold temperatures on the ability of EAB to disperse. This is an important component in understanding how Minnesota winters will affect the rate of spread and ultimately the impact of EAB.

Summary Budget Information for Activity 2, UMN – Part B:	**ENRTF Budget:**	**$ 149,250**
	Amount Spent:	**$ 147,366**
	Balance:	**$ 1,884**

Activity Completion Date:

Outcome	**Completion Date**	**Budget**
1. Measure effect of cold on EAB lipid content and create model.	June, 2016	$ 73,375
2. Measure relationship between air and within-tree temperatures and create model.	June, 2016	$ 75,875

Activity Status as of November 15, 2013**:**
We have secured logs infested with emerald ash borer larvae to study, but have not yet conducted any cold temperature testing. Testing will begin this winter.

Activity Status as of May 15, 2014**:**
Surveys during the North Dakota EAB field visit hosted by MDA (see Dissemination events in MDA report) indicated that cold temperatures killed between 60-70% of overwintering larvae under field conditions this winter. As we continue to gain an understanding of mortality-temperature relationships, we will be able to begin lipid content analyses.

Activity Status as of November 15, 2014**:**
No winter cold temperature testing was completed during this past summer. Graduate student Lindsey Christiansen, trained during the first phase of the LCCMR EAB biocontrol grant (2011-2014), is finishing her work on mortality-temperature relationships of EAB in different hosts.

Activity Status as of May 15, 2015:
Dylan Tussey was admitted as a Master's student to the Entomology graduate program at the University of Minnesota. Dylan will be investigating the sublethal effects of cold on emerald ash borer. He began in January 2015.

Lipid extraction methods. Preliminary research has focused on the refinement of methods to extract lipids from different developmental stages of emerald ash borer. This insect develops from an egg through four instars. The final (fourth) instar undergoes distinct morphological changes without molting. These additional "stages" are commonly known as "J-stage" and "fat-head" larvae. The fat-head stage immediately precedes pupation and subsequent adult emergence. Emerald ash borer typically overwinter as J-stage (most common) or as first or second (early) instars or third or fourth (late) instars.

We rely on a petroleum ether method of extraction that has been used to extract lipids from bark beetles (McKee and Aukema 2015[1]). However, later instar larvae and adults are considerably larger than bark beetles, so the objective was to determine the length of time necessary to extract all lipids.

Three insect sources were used for these studies. First, lipids were extracted from air-dried, preserved adult specimens of adult emerald ash borer. These individuals had been collected in 2013. Second, lipids were extracted from adult beetles that had been collected in June 2014 from infested trees harvested from Great River Bluffs State Park. These insects were collected within 72 hours of emergence, weighed, and immediately frozen at -80°C. Finally, larvae were collected in March 2015 from ash logs that originated at two sites in St. Paul, MN. Larvae were categorized as early instar (1st & 2nd), late instar, J-stage, or fathead and immediately weighed.

All insects were oven-dried at approximately 60°C for 24 hours. Dry weights were obtained by weighing insects within one hour of removal from the oven to minimize rehydration from ambient humidity.

Lipid extractions for adults and larvae were performed using 300mL of petroleum ether circulating through an extraction column and condenser with a round-bottomed flask heated to ~45° C. Individuals were placed in modified 0.5 mL microcentrifuge tubes with labels. When necessary, larger larvae were bisected to fit in the microcentrifuge tubes. Bisected larvae were recorded and compared to whole larvae for differences. Extractions ran with two flushes of the extractor column per hour. In general, total extraction time was determined by extracting lipids for a predetermined period, drying the insects for 24 hours at 60° C, and weighing the insects. This general process was repeated multiple times with the same individuals. The dry weights of individuals before and after each extraction were compared, and extractions continued until no significant weight difference ($P<0.05$; paired t-test) was observed.

After the final lipid extraction, lipid weight was determined by subtracting the final post-lipid-extraction, dry weight from the initial dry weight. Percent lipid content for each EAB was calculated by dividing the mass of lipid by the initial dry weight.

Total extraction time was determined to be 16 hours for adults and early-instars with no significant difference in lipid weights between 16 h and 20 h (P-value: 0.358). J-stages, fat-heads, and late instars require longer extraction times. Figure 1 shows the mean± SE of percent lipid of dry mass of adults and larvae.

Figure 1. Lipid content of emerald ash borer life stages.

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[1] McKee, F. and B.H. Aukema. 2015. Influence of temperature on the reproductive success, brood development and brood fitness of the eastern larch beetle *Dendoctonus simplex* LeConte. Agricultural and Forest Entomology 17: 102-112.

Sublethal effects of cold exposure. Infested ash trees were harvested from Great River Bluffs State Park (Winona County) and two locations in St. Paul during January and February 2015. Adult beetles are currently being collected from these logs for tests to be conducted this spring and summer.

Activity Status as of November 15, 2015: A total of 152 adult emerald ash borer adults were used in this part of the study. We began by examining the effect of feeding on lipid content and the effect of lipid content on flight capacity. Green ash trees that were naturally infested with emerald ash borer larvae were cut from two sites in St. Paul and one in Great River Bluffs State Park. Cut logs were held in cardboard rearing tubes to allow adult beetles to emerge naturally. Beetles were collected daily, and the sex of each individual was immediately determined. Beetles were placed in plastic rearing containers that had been fitted with a floral pick. The pick kept a terminal leaflet of *Fraxinus uhdei* fresh for adult consumption. *Fraxinus uhdei* is a, tropical evergreen ash that grows well in the greenhouse, and thus, has become a standard host for rearing emerald ash borer in the laboratory. After feeding, the leaves are scanned to determine how much area is missing (i.e., consumed by the insects) .Leaves were replaced as necessary, Beetles were assigned randomly to different feeding treatments. The treatments were a predetermined period of feeding. All emerald ash borers are then weighed when they finish eating to obtain fresh weights. Approximately one-half of the total number of adults are frozen to measure lipid content. The other half are put on the laboratory flight mill for 24 hours. At the end of 24 hours, they are weighed again and frozen to determine lipid content. From flight mill recordings, we can determine the number of bouts of flight, flight velocity, and flight distance, among other flight characteristics. Lipid extraction takes place as above.

We are finding that three patterns are emerging:

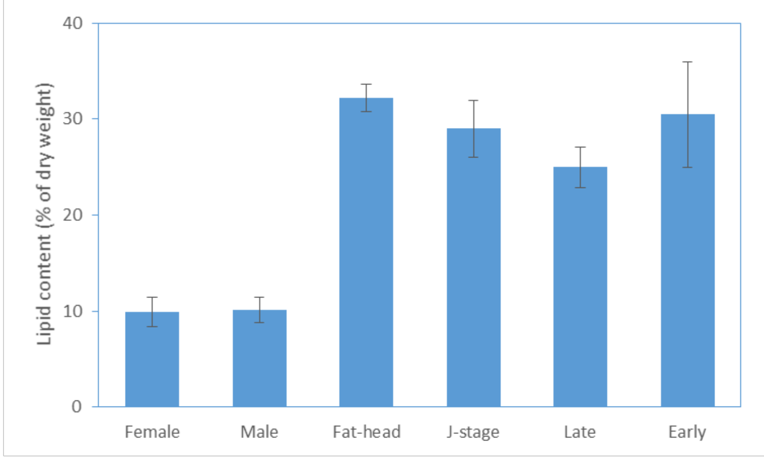
- Male and female beetles have similar lipid contents
- Adult feeding does increase dry weight, but not necessarily lipid content
- Emerald ash borers that consume more food tend to fly shorter distances

Additional details appear in the attached poster.

These results are being presented at the Entomological Society of America meeting next week.

More infested green ash was collected from St. Paul, MN to repeat this study during the winter of 2015-2016.

Activity Status as of May 15, 2016:



We are currently in the process of repeating and expanding the first year of the study by taking three complementary approaches. First, in a repeat of the study that was conducted in the spring of 2015, we are evaluating the relationship between energy reserves, adult feeding, and flight capacity. We initially focused exclusively on lipids because the literature suggests this energy source fuels flight in many insects. However, glycogen may also be an important fuel source, so we will expand our biochemical analyses to measure quantities of this fuel in adult insects. These studies are essential to establish relationships between fuel levels and flight capacity. For this study, infested trees were harvested in Minneapolis and St. Paul in late fall of 2015 and held outdoors on the St. Paul campus. Early this spring, the logs were placed in rearing tubes to allow us to collect emerging EAB adults. Emergence began in late April.

In the second study, we are evaluating the impact of different winter temperature regimes on lipid content of EAB larvae, and possibly glycogen if our methods will allow. Infested ash trees were harvested in Minnesota and Ohio. Under permits from USDA APHIS, in early January, half of the logs from Minnesota were taken to Ohio, and half of the logs from Ohio were brought to Minnesota. Logs were held in unheated restricted spaces in both locations. In March, logs were peeled to collect EAB larvae. Supercooling point, a measure of the temperature at which an insect begins to freeze, was measured for each larva. Larvae were preserved for later lipid analysis. (The costs of harvesting these trees, transporting the trees, and collecting larvae were paid by the USDA Forest Service – Northern Research Station; the biochemical analysis is an add-on to this larger experiment.)

The third study is a hybrid between the previous two. The study is designed to test the effects of winter severity and foliage feeding on energy levels (lipids and glycogen) and flight capacity of EAB adults. Infested logs were harvested in Minneapolis and St. Paul. Approximately 30 logs were held outdoors in St. Paul and another 30 were held outdoors in Grand Rapids, MN. All logs were returned to St. Paul. Average temperatures in Grand Rapids were approximately 3°C colder than in St. Paul, while the average daily low was 9°C colder. Logs have been placed in emergence tubes to collect adult EAB. We will measure lipid an glycogen levels on adults from both locations after allowing them to feed on ash leaves for 0 – 14 days and before or after flight.

Activity Status as of November 15, 2016:

We continued leaf-feeding assays and presented our results at two conferences (see dissemination). Adult feeding did not increase lipid content, a common measure of energy reserves. We did find, however, that there was a slight increase in sugar and glycogen content of the insects when they fed on more ash leaves. The insects feeding behavior was very similar independent of which site the insects had overwintered. Regardless of whether the insects overwintered in logs in St. Paul or the colder location of Grand Rapids, the insects fed at the same rate when they emerged from the logs. Insects are typically apt to fly for several days post-emergence, but insects that have flown have lower glycogen contents. We are now working to elucidate how colder temperatures may or may not limit spread though different mechanisms of reduced movement vs. strict mortality of individual insects.

Final Report Summary:

We have found that cold temperatures do not limit spread by virtue of reduced movement or dispersal capacity in the spring, contrary to our original hypothesis. Instead, it appears that cold temperatures simply affect ultimate survival, but those that do survive the winter show no ill effects that would be manifested in reduced flight. Adult glycogen content declined with flight and increased only slightly with feeding. Overwintering location affected survival rates, but not energy reserves or flight capacity. These results suggest that flight capacity of *A. planipennis* is largely determined at emergence.

We are submitting this work to a peer-reviewed journal and will forward the eventual publication to LCCMR for inclusion in project files.

V. DISSEMINATION:

Description:

The primary audience for this work will be municipalities and other entities responsible for managing EAB at the local level. There are many opportunities to address this audience through meetings held throughout the year, both at MDA through the EAB Forum (bimonthly meeting) and also through conferences and meetings held

around the state throughout the year. MDA is often invited to provide information about EAB at these meetings and conferences which is likely to continue in the future.
We anticipate that this work will result in the development of guidelines or documents meant to convey the findings of this work and what it means for local level management of EAB. In addition, we expect that this work will result in articles in scientific journals as well as presentations at national scientific meetings. However, ENRTF funds will not be used for travel to national meetings. Significant findings through this work may be communicated through the news media as well as social media.

Status as of November 15, 2013**:**

See MDA Project Report for description.

Status as of May 15, 2014**:**

See MDA Project Report for description.

Status as of November 15, 2014**:**
In addition to the presentations listed in the MDA report, this work was highlighted by the project lead at the

- Southern Forest Insect Work Conference, July 22-25, Charleston, SC
- Upper Midwest Invasive Species Conference, October 22-24, Duluth, MN

Status as of May 15, 2015**:**
In addition to the presentations listed in the MDA report, this work was highlighted by the project lead at the
Entomological Society of America Annual Meeting, Nov 16-19, Portland, OR

Status as of November 15, 2015**:**
In addition to the presentations listed in the MDA report, this work was highlighted at:

Tussey, D. A., B.H. Aukema, and R.C. Venette. 2015. Effects of feeding on lipid content and dispersal capability of adult *Agrilus planipennis*. North Central Forest Pest Workshop, Mosinee Indian Reservation, Keshena, WI, Sept 24-27, 2015 (Poster; see attached).

Tussey, D.A., B.H. Aukema, and R.C. Venette. 2015. Effects of age and feeding on lipid content and flight capacity of *Agrilus planipennis*. Department of Entomology, University of Minnesota, St. Paul, MN, November 10, 2015. (1st prize for poster presentation).

This research will be presented at the upcoming national meeting of the Entomological Society of America.

Activity Status as of May 15, 2016:
Tussey, D.A., B.H. Aukema, and R.C. Venette. 2015. Effects of age and feeding on lipid content and flight capacity of *Agrilus planipennis*. National meeting of the Entomological Society of America, Minneapolis, MN, November 16, 2016 (Poster)

Tussey, D.A. 2016. Effects of winter severity on emerald ash borer nutrition levels and flight performance. Department of Entomology seminar series, University of Minnesota, St. Paul, MN. May 10, 2016

Activity Status as of Nov 15, 2016:

- Upper Midwest Invasive Species Conference, October 18 – Joint presentation with MDA collaborators; Mark Abrahamson provided a 20 minute presentation on the project and summarized the results demonstrating that all sampling methods were useful for detecting EAB before significant tree damage at study sites.

- Graduate student Dylan Tussey presented work from Activity 3 (cold tolerance) at the International Congress of Entomology in Orlando, Florida September 24-27, 2016. No project funds were used for this travel.

Final Report Summary:

We worked closely with the MDA to disseminate this work; see the sibling MDA project summary for details. The primary audience for this work was disseminated to municipalities and other entities responsible for managing EAB at the local level. Information was conveyed through meetings held throughout the year, both at MDA through the EAB Forum (bimonthly meeting) and also through conferences and meetings held around the state throughout the year and also at professional and technical conferences.

In addition to regional spring EAB meetings (Blaine, Rochester, Duluth), summaries of these results were recently provided in presentations to 170 attendees at the Workshop on the Future of Ash Forests, July 25-27, 2017 in Duluth.

VI. PROJECT BUDGET SUMMARY:

A. ENRTF Budget:

University of Minnesota

Budget Category	$ Amount	Explanation
Personnel:	~~$ 348,000~~ $ 354,093	One person (Dr. Aukema) for 3 years of faculty summer salary = $64,000 • 1.6 month/year + benefits One ~~Two~~ 3 year FTE graduate students = $240,000 • mean salary of $21,300 + fringe + tuition @ $13,300 = $40,000/year/student Two undergraduate students = $44,000 • $12/hour for 14 weeks at 40 hours/week + 8% benefits for 2 students for 3 years We were able to engage additional personnel on the project (lab technician, postdoc) due to reduced graduate student time (shifting to leveraged and related federal project).
Equipment/Tools/Supplies:	~~$ 2,500~~ $ 596	Temperature sensors for recording within tree winter temperatures ~25 @ $100 each
Travel Expenses in MN:	~~$ 7,500~~ $ 4,991	Vehicle rental and fuel = $1,500 • Mileage for vehicle rental and fuel at $500 /year for 3 years – as described above in the MDA budget, the most cost efficient means of travel will be utilized Meals and Lodging = $6,000 • Approximately 15 days of travel/year for 3 years for 4 employees - 2 undergrad students, 2 grad students, and approximately 5 days of travel/year for 3 years for 2 of the co-principal investigators
Other:	~~$ 2,000~~	Publications including approximately 2 journal articles

	$ 320	($500-$1,000 each), scientific meeting posters (2 @ $200 each) Cost savings were realized by new poster printer in-house after start of project and reduced publication fees.
TOTAL ENRTF BUDGET:	**$ 360, 000**	**Balance of $ 1,884 returned to ENRTF**

Explanation of Use of Classified Staff:
N/A

Explanation of Capital Expenditures Greater Than $3,500:
N/A

Number of Full-time Equivalent (FTE) funded with this ENRTF appropriation:
MDA Coordinator: 3 years @ 32 hours / week = 4,992 total hours
UM Faculty Advisor: 3 years @ 1.6 months / year = 832 total hours
Graduate Students: 2 students for 3 years @ 2080 hours year = 12,480 total hours
Undergraduate Student Workers or Technicians: 2 students for 3 years @ 14 weeks per year = 3,360 total hours
Total Hours = 16,672
Total FTE's = 16,672 hours / 2080 hours per year = 8.02

Number of Full-time Equivalent (FTE) estimated to be funded through contracts with this ENRTF appropriation:
N/A

B. Other Funds:

Source of Funds	$ Amount Proposed	$ Amount Spent	Use of Other Funds
Non-state - federal APHIS grants 2015-2016	$0	$63,480	After the project started, we successfully leveraged project funds for these grants. We used these funds for an extensive computational analysis of the efficacy of removing trees when detected early.
State			
Field equipment, lab equipment and lab space, computing/software, GIS and data management ($40,000 for U of M), graduate student advising and research management ($100,000 at U of M)	$140,000	$	
TOTAL OTHER FUNDS:	**$140,000**	**$63,480**	

VII. PROJECT STRATEGY:

A. Project Partners:

Receiving funds: Improving EAB detection is a collabrotive effort between MDA (**receiving $240,000**) and University of Minnesota (**receiving $360,000**). MDA will oversee Part A of the project and coordinate detection work among project partners and cooperators. U of M will oversee Part B of the project and lead research efforts for both evaluating EAB detection efficacy and evaluating the impact of temperature on dispersal capability of EAB. Other EAB projects at MDA will be leveraged to support this work where common goals are found. Both MDA and U of M will supply in-kind support through facilities, IT support, equipment and intellectional input.

Cooperators on this project will include entities with EAB infestations on or adjacent to their jurisdiction such as the cities of St Paul, Minneapolis and Shoreview, Ramsey County, DNR and DOT. We will work with cooperators to implement detection activities within their jurisdictions – particularly in the removal of branches for EAB sampling. Some cooperators may be able to donate their time for this work in-kind, other cooperators will be reimbursed for their services using ENRTF funds (**$75,000** total among all cooperators for the entire project – these funds will be passed through from the amount designated for MDA).

Not receiving funds: US Forest Service will provide in-kind support through use of facilities, equipment and intellectual input. Some cooperators at the local level will provide in-kind support through the use of staff and equipment as described above. Like other EAB work within Minnesota, the progress of this project will be shared with a wide group of stakeholders including federal and state agencies, local governments and industry groups.

B. Project Impact and Long-term Strategy:

A more thorough understanding of the capabilities and limitations of detection techniques for EAB will provide a more solid basis for local governments and other entities in making management decisions related to EAB. For instance, current recommendations on when to begin chemical treatment for EAB indicate that trees within 10-15 miles of known EAB infestations are at significant risk of becoming infested and should be considered for treatment. However, our experience in Minnesota indicates that a much tighter buffer should be considered around infested trees which would potentially lead to fewer chemicals used but with greater impact due to concentrating efforts where they are truly needed.

Municipalities are at great risk from EAB due to the heavy reliance on ash in urban areas. Currently, there are no guidelines based on quantitative studies as to what the most efficacious technique for EAB detection is, and what the results from using a given technique mean. Consequently, municipalities are left without good information for detecting EAB and consequently without good information for making decisions related to EAB management.

The outcomes from this project should provide municipalities and other local land managers in Minnesota with the information they need to more confidently assess the presence/absence or distribution of EAB in their community and as a result to plan the most appropriate management actions.

C. Spending History:

N/A

VIII. ACQUISITION/RESTORATION LIST:

N/A

IX. MAP(S):

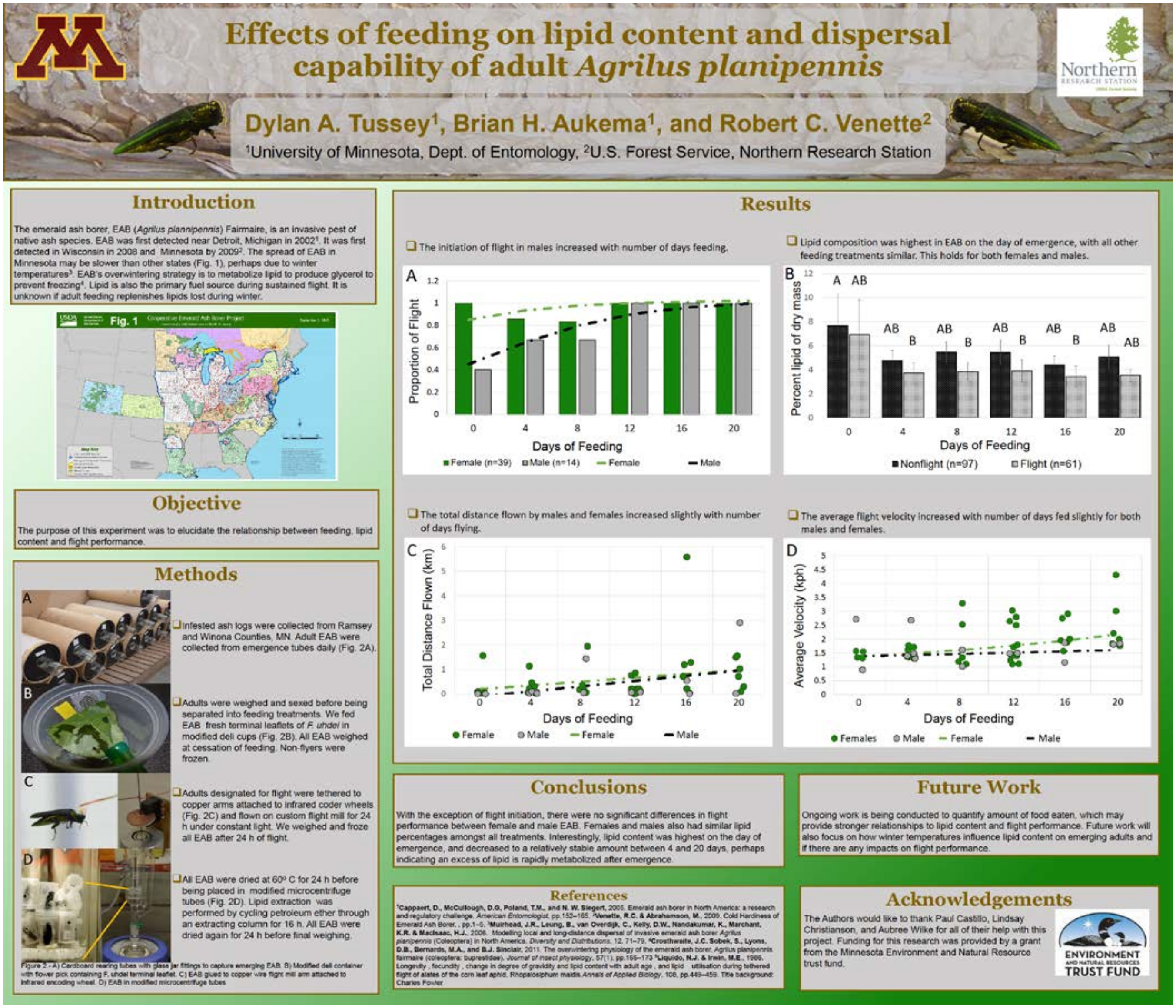
N/A

X. RESEARCH ADDENDUM:

N/A

XI. REPORTING REQUIREMENTS:

Periodic work plan status update reports will be submitted not later than November 15, 2013, May 15, 2014, November 15, 2014, May 15, 2015, and November 15, 2015. A final report and associated products will be submitted between June 30 and August 15, 2016 as requested by the LCCMR.



Effects of feeding on lipid content and dispersal capability of adult *Agrilus planipennis*

Dylan A. Tussey[1], Brian H. Aukema[1], and Robert C. Venette[2]
[1]University of Minnesota, Dept. of Entomology, [2]U.S. Forest Service, Northern Research Station

Introduction

The emerald ash borer, EAB (*Agrilus plannipennis*) Fairmaire, is an invasive pest of native ash species. EAB was first detected near Detroit, Michigan in 2002[1]. It was first detected in Wisconsin in 2008 and Minnesota by 2009[2]. The spread of EAB in Minnesota may be slower than other states (Fig. 1), perhaps due to winter temperatures[3]. EAB's overwintering strategy is to metabolize lipid to produce glycerol to prevent freezing[4]. Lipid is also the primary fuel source during sustained flight. It is unknown if adult feeding replenishes lipids lost during winter.

Objective

The purpose of this experiment was to elucidate the relationship between feeding, lipid content and flight performance.

Methods

❑ Infested ash logs were collected from Ramsey and Winona Counties, MN. Adult EAB were collected from emergence tubes daily (Fig. 2A).

❑ Adults were weighed and sexed before being separated into feeding treatments. We fed EAB fresh terminal leaflets of *F. uhdei* in modified deli cups (Fig. 2B). All EAB weighed at cessation of feeding. Non-flyers were frozen.

❑ Adults designated for flight were tethered to copper arms attached to infrared coder wheels (Fig. 2C) and flown on custom flight mill for 24 h under constant light. We weighed and froze all EAB after 24 h of flight.

❑ All EAB were dried at 60° C for 24 h before being placed in modified microcentrifuge tubes (Fig. 2D). Lipid extraction was performed by cycling petroleum ether through an extracting column for 16 h. All EAB were dried again for 24 h before final weighing.

Figure 2 - A) Cardboard rearing tubes with glass jar fittings to capture emerging EAB. B) Modified deli container with flower pick containing F. uhdei terminal leaflet. C) EAB glued to copper wire flight mill arm attached to infrared encoding wheel. D) EAB in modified microcentrifuge tubes

Results

❑ The initiation of flight in males increased with number of days feeding.

❑ Lipid composition was highest in EAB on the day of emergence, with all other feeding treatments similar. This holds for both females and males.

❑ The total distance flown by males and females increased slightly with number of days flying.

❑ The average flight velocity increased with number of days fed slightly for both males and females.

Conclusions

With the exception of flight initiation, there were no significant differences in flight performance between female and male EAB. Females and males also had similar lipid percentages amongst all treatments. Interestingly, lipid content was highest on the day of emergence, and decreased to a relatively stable amount between 4 and 20 days, perhaps indicating an excess of lipid is rapidly metabolized after emergence.

Future Work

Ongoing work is being conducted to quantify amount of food eaten, which may provide stronger relationships to lipid content and flight performance. Future work will also focus on how winter temperatures influence lipid content on emerging adults and if there are any impacts on flight performance.

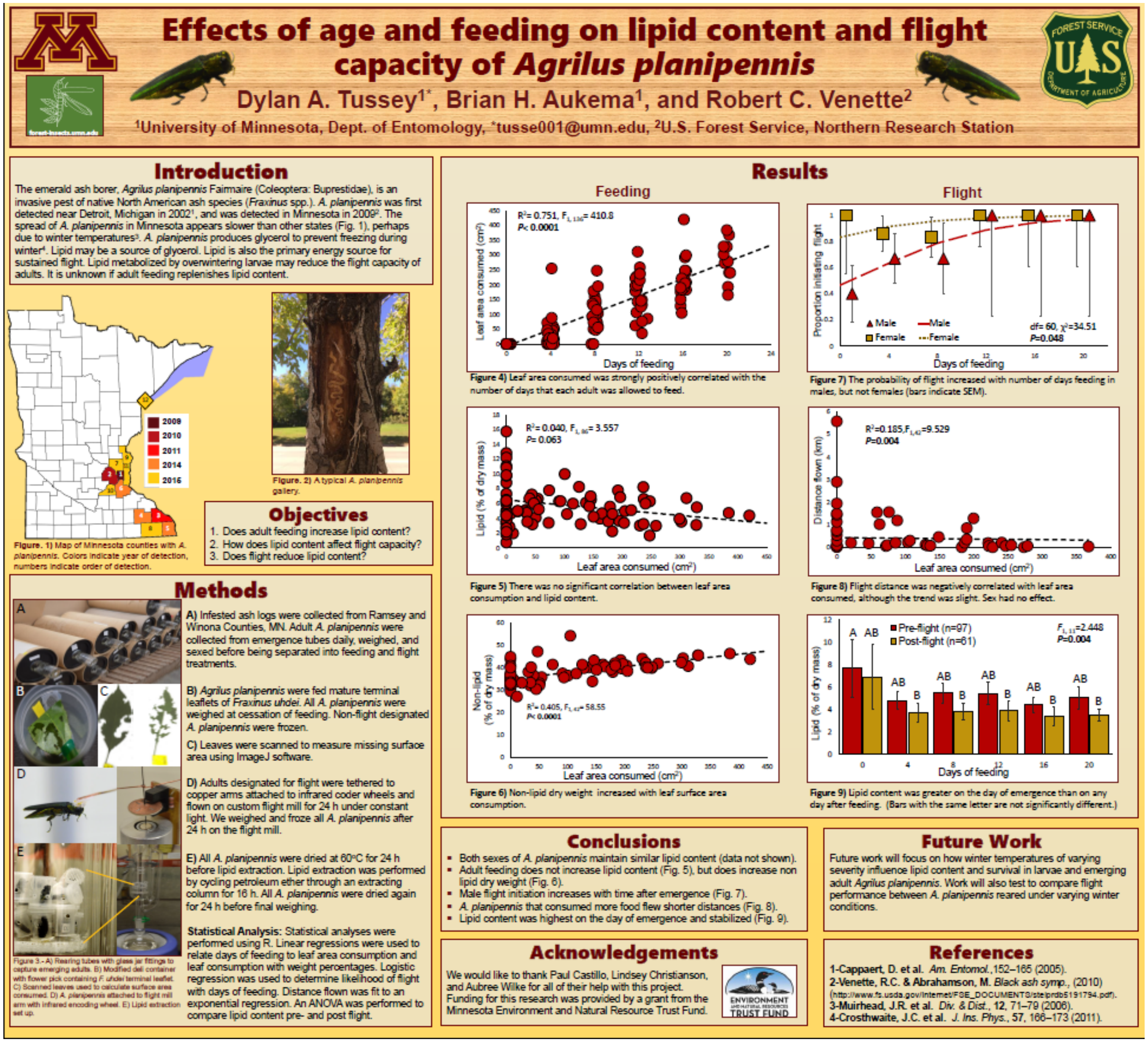
References

[1]**Cappaert, D., McCullough, D.G, Poland, T.M., and N. W. Siegert**, 2005. Emerald ash borer in North America: a research and regulatory challenge. *American Entomologist*, pp.152–165. [2]**Venette, R.C. & Abrahamson, M.**, 2009. Cold Hardiness of Emerald Ash Borer, , pp.1–5. [3]**Muirhead, J.R., Leung, B., van Overdijk, C., Kelly, D.W., Nandakumar, K., Marchant, K.R. & MacIsaac, H.J.**, 2006. Modelling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America. *Diversity and Distributions*, 12, 71–79. [4]**Crosthwaite, J.C. Sobek, S., Lyons, D.B., Bernards, M.A., and B.J. Sinclair**, 2011. The overwintering physiology of the emerald ash borer, *Agrilus planipennis* fairmaire (coleoptera: buprestidae). *Journal of insect physiology*, 57(1), pp.166–173 [5]**Liquido, N.J. & Irwin, M.E.**, 1986. Longevity , fecundity , change in degree of gravidity and lipid content with adult age , and lipid utilisation during tethered flight of alates of the corn leaf aphid, Rhopalosiphum maidis *Annals of Applied Biology*, 108, pp.449–459. Title background: Charles Fowler

Acknowledgements

The Authors would like to thank Paul Castillo, Lindsay Christianson, and Aubree Wilke for all of their help with this project. Funding for this research was provided by a grant from the Minnesota Environment and Natural Resource trust fund.

Presented at the North Central Forest Pest Workshop to forest health professionals from the Upper Midwest and central Canada.



Effects of age and feeding on lipid content and flight capacity of *Agrilus planipennis*

Dylan A. Tussey[1*], Brian H. Aukema[1], and Robert C. Venette[2]

[1]University of Minnesota, Dept. of Entomology, *tusse001@umn.edu, [2]U.S. Forest Service, Northern Research Station

Introduction

The emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), is an invasive pest of native North American ash species (*Fraxinus* spp.). *A. planipennis* was first detected near Detroit, Michigan in 2002[1], and was detected in Minnesota in 2009[2]. The spread of *A. planipennis* in Minnesota appears slower than other states (Fig. 1), perhaps due to winter temperatures[3]. *A. planipennis* produces glycerol to prevent freezing during winter[4]. Lipid may be a source of glycerol. Lipid is also the primary energy source for sustained flight. Lipid metabolized by overwintering larvae may reduce the flight capacity of adults. It is unknown if adult feeding replenishes lipid content.

Figure. 1) Map of Minnesota counties with *A. planipennis*. Colors indicate year of detection, numbers indicate order of detection.

Figure. 2) A typical *A. planipennis* gallery.

Objectives

1. Does adult feeding increase lipid content?
2. How does lipid content affect flight capacity?
3. Does flight reduce lipid content?

Methods

A) Infested ash logs were collected from Ramsey and Winona Counties, MN. Adult *A. planipennis* were collected from emergence tubes daily, weighed, and sexed before being separated into feeding and flight treatments.

B) *Agrilus planipennis* were fed mature terminal leaflets of *Fraxinus uhdei*. All *A. planipennis* were weighed at cessation of feeding. Non-flight designated *A. planipennis* were frozen.

C) Leaves were scanned to measure missing surface area using ImageJ software.

D) Adults designated for flight were tethered to copper arms attached to infrared coder wheels and flown on custom flight mill for 24 h under constant light. We weighed and froze all *A. planipennis* after 24 h on the flight mill.

E) All *A. planipennis* were dried at 60ºC for 24 h before lipid extraction. Lipid extraction was performed by cycling petroleum ether through an extracting column for 16 h. All *A. planipennis* were dried again for 24 h before final weighing.

Statistical Analysis: Statistical analyses were performed using R. Linear regressions were used to relate days of feeding to leaf area consumption and leaf consumption with weight percentages. Logistic regression was used to determine likelihood of flight with days of feeding. Distance flown was fit to an exponential regression. An ANOVA was performed to compare lipid content pre- and post flight.

Figure 3.- A) Rearing tubes with glass jar fittings to capture emerging adults. B) Modified deli container with flower pick containing *F. uhdei* terminal leaflet. C) Scanned leaves used to calculate surface area consumed. D) *A. planipennis* attached to flight mill arm with infrared encoding wheel. E) Lipid extraction set up.

Results

Figure 4) Leaf area consumed was strongly positively correlated with the number of days that each adult was allowed to feed.

Figure 5) There was no significant correlation between leaf area consumption and lipid content.

Figure 6) Non-lipid dry weight increased with leaf surface area consumption.

Figure 7) The probability of flight increased with number of days feeding in males, but not females (bars indicate SEM).

Figure 8) Flight distance was negatively correlated with leaf area consumed, although the trend was slight. Sex had no effect.

Figure 9) Lipid content was greater on the day of emergence than on any day after feeding. (Bars with the same letter are not significantly different.)

Conclusions

- Both sexes of *A. planipennis* maintain similar lipid content (data not shown).
- Adult feeding does not increase lipid content (Fig. 5), but does increase non lipid dry weight (Fig. 6).
- Male flight initiation increases with time after emergence (Fig. 7).
- *A. planipennis* that consumed more food flew shorter distances (Fig. 8).
- Lipid content was highest on the day of emergence and stabilized (Fig. 9).

Future Work

Future work will focus on how winter temperatures of varying severity influence lipid content and survival in larvae and emerging adult *Agrilus planipennis*. Work will also test to compare flight performance between *A. planipennis* reared under varying winter conditions.

Acknowledgements

We would like to thank Paul Castillo, Lindsey Christianson, and Aubree Wilke for all of their help with this project. Funding for this research was provided by a grant from the Minnesota Environment and Natural Resource Trust Fund.

References

1-Cappaert, D. et al. *Am. Entomol.*,152–165 (2005).
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Presented at the national meeting of the Entomological Society of America to experts on emerald ash borer, insect physiology, and insect management.

Attachment A: Budget Detail for M.L. 2013 Environment and Natural Resources Trust Fund Projects

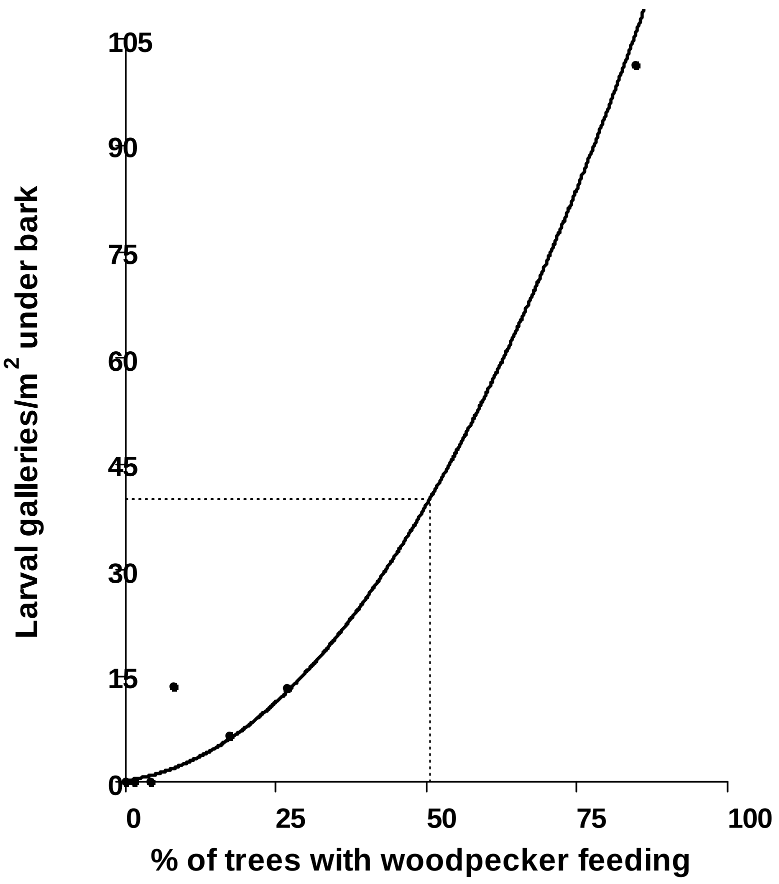
Project Title: Improving Emerald Ash Borer Detection Efficacy for Control
Legal Citation: M.L. 2013, Chp. 52, Sec. 2, Subd. 06cB
Project Managers: Brian Aukema @ U of M
M.L. 2013 ENRTF Appropriation: $ 600,000 between MDA ($240,000) and U of M ($360,000)
Project Length and Completion Date: 3 year project with one year approved extension to June 30, 2017

ENVIRONMENT AND NATURAL RESOURCES TRUST FUND BUDGET	**Activity 1 Budget**	**Revised Activity Budget 08/31/17**	**Amount Spent**	**Balance**	**Activity 2 Budget**	**Revised Activity Budget 08/31/17**	**Amount Spent**	**Balance**	**TOTAL ORIGINAL BUDGET**	**TOTAL REVISED BUDGET**	**TOTAL SPENT**	**TOTAL BALANCE**
BUDGET ITEM	**Implement detection surveys for EAB to evaluate efficacy of different detection techniques under different abundances of EAB.**				**Implement field and laboratory experiments to examine factors affecting dispersal distances and winter survival of EAB**							
Personnel (Wages and Benefits) - Direct appropriation to U of M												
- U of M Faculty Advisor: (79% salary, 21% fringe), 13% FTE (estimated $64,000) - U of M Graduate Students: Two students (47% salary, 53% fringe including tuition), 200% FTE (estimated $120,000) - U of M student workers: Two students/techs (92% salary, 8% fringe), 54% FTE (estimated $22,000)	~~$206,000~~	$207,684	$207,684	$0	~~$142,000~~	$146,409	$146,409	$0	$348,000	$354,093	$354,093	$0
Equipment/Tools/Supplies - Direct appropriation to U of M												
Temperature sensors for recording within tree winter temperatures - 25 @ ~100 each				$0	~~$2,500~~	$596	$596	$0	$2,500	$596	$596	$0
Travel expenses in Minnesota - Direct appropriation to U of M												
- Vehicle rental and fuel (estimated $750) - Meals and lodging for 2 graduate students and 2 undergraduate students (15 days of travel per year for 3 years) and approximately 5 days of travel per year for 3 years for 2 co-principal invesigators (estimated $3,000	~~$3,750~~	$2,746	$2,746	$0	~~$3,750~~	$2,245	$361	$1,884	$7,500	$4,991	$3,106	$1,885
Other - Direct appropriation to U of M												
Publications include approximately 2 journal articles ($500 - $1000 each), scientific meeting posters (2 @ $200 each)	~~$1,000~~	$320	$320	$0	~~$1,000~~	$0		$0	$2,000	$320	$320	$0
COLUMN TOTAL	**~~$210,750~~**	**$210,750**	**$210,750**	**$0**	**~~$149,250~~**	**$149,250**	**$147,366**	**$1,884**	**$360,000**	**$360,000**	**$358,116**	**$1,884**

Improving Emerald Ash Borer Detection Efficacy for Control

Detecting new infestations of emerald ash borer is hard. Really hard.

Woodpeckers feed on developing larvae, and can find them faster than people notice the infested trees. The best way to find new infestations of emerald ash borer is to measure what percentage of local trees have feeding. If it's less than 50%, we now know that there will likely be less than 40 larvae per square meter under the bark, and the tree may be saved.



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Strategic removal of host trees in isolated, satellite infestations of emerald ash borer can reduce population growth

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ABSTRACT

Emerald ash borer is an invasive beetle causing significant mortality of ash trees (*Fraxinus* spp.) in North America and western Russia. The invasive range has expanded to more than half of the states in the United States since the initial detection in Michigan, USA in 2002. Emerald ash borer is typically managed with a combination of techniques including surveys/trapping, insecticide treatments, host tree removal, biological control, and public education/outreach. The insect's rapid spread rate and cryptic life history and a lack of resistance among most North American *Fraxinus* spp. have limited opportunities to gather empirical data on how aggressive tree removal may slow population growth in isolated, satellite infestations if detected early. An early detection of an isolated population of emerald ash borer in 2009 in Minnesota, USA was managed by using a selective host-tree removal program (i.e., sanitation). Trees were preferentially removed based on the assumption that evidence of woodpecker foraging (i.e., pecking) was a good indicator of infestation by emerald ash borer. Extensive sampling and survey data on larval densities and the presence/absence of pecking on ash trees in a 6-km^2 area for the Twin Cities, Minnesota were used to parameterize a model of population growth over the next four years. We found that removing ~63% of the total trees across four years reduced the cumulative number of beetles produced in the core infested area by ~54%. However, we also found that increases in efficacy, i.e., larger decreases in beetle production per removed tree, could be achieved by preferentially removing trees with pecking. The invasive range of emerald ash borer in North America and western Russia continues to expand via natural and human-aided dispersal. While silvicultural control tactics alone will not be an adequate management strategy, tree removal is an important component of both a broader pest management program and the systematic replacement of ash canopies in urban forests. Increasing understanding of the efficacy of different management techniques in slowing population growth of emerald ash borer will be useful to support decision–making by land managers.

1. Introduction

Invasions and range expansions by alien or native species create global challenges. Invasive alien species cause severe ecological and evolutionary impacts across a range of ecosystems with economic impacts totaling $150 billion in damages and losses in the United States alone per annum (Mooney and Cleland 2001; Pimentel et al., 2005; Pejchar and Mooney, 2009). Increases in international trade and globalization have been positively correlated with establishment rates of non-native species in North America (Levine and D'Antonio, 2003; Hulme, 2009; Aukema et al., 2010; Huang et al., 2011). Within invaders from the class Insecta, over half of new insects detected in the United States from 1980 to 2006 were classified as phloem- or wood-boring (Aukema et al., 2010). Between 1985–2005, for example, at least 25 new species of phloem or wood-boring beetles became established in the United States (Haack, 2006). Several *Agrilus* spp. (Coleoptera: Buprestidae), referred to as flat-headed borers, have emerged as destructive native and alien pests of hardwoods in both the United States and Europe (e.g., Coleman et al., 2012; Brown et al., 2014; Herms and McCullough, 2014).

The emerald ash borer *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) is an invasive pest native to eastern Russia and China that was discovered causing widespread mortality of ash trees (Oleaceae: *Fraxinus* spp.) near Detroit, MI, USA in 2002 (Haack et al., 2002; Poland and McCullough, 2006; Herms and McCullough, 2014). The initial introduction near Detroit likely occurred in the early to mid 1990s

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(Siegert et al., 2014). The discovery of emerald ash borer in North America was followed by the detection of another invasion by this insect in Moscow, Russia in 2003 (Baranchikov et al., 2008). The invasive range of emerald ash borer in North America has since expanded to include two Canadian provinces and more than twenty states in the central and eastern half of the contiguous United States (Herms and McCullough, 2014). The expansion of the invasive range is due in part to natural dispersal via the strong-flying adults (Mercader et al., 2009; Siegert et al., 2010; Taylor et al., 2010; Fahrner et al., 2015), whereas long range dispersal is primarily driven by the human-mediated movement of firewood (BenDor et al., 2006; Herms and McCullough, 2014). Most species of ash appear highly susceptible to infestation by emerald ash borer (Herms and McCullough, 2014) and most of the North American continent where *Fraxinus* spp. occur remains at risk.

Following a new detection of an invasive phloem or wood-boring insect, there are several management options available (Brockerhoff et al., 2006; El-Sayed et al., 2006; Brockerhoff et al., 2010; Suckling et al., 2012). If the invader is detected soon after establishment and the area infested is sufficiently confined, eradication may be attempted via a combination of insecticides, trapping/surveys, host plant removal, and public outreach (Haack et al., 2010; Suckling et al., 2012). For example, Asian long-horned beetle has been successfully eradicated from urban sites in Japan and Chicago, IL, USA using a combination of these methods (Haack et al., 2010; Liebhold et al., 2016). However, similar concerted attempts to eradicate emerald ash borer from the site of initial establishment failed (Herms and McCullough, 2014). No successful eradications of emerald ash borer have ever been reported, likely due to its endophytic larval life history and difficulties in detecting low-density infestations (Tobin et al., 2014; Herms and McCullough, 2014).

When eradication fails, efforts shift to reducing populations of the pest below ecologically and/or economically damaging levels. A pilot project called SLAM (**SL**ow **A**sh **M**ortality) was initiated as a management strategy in 2008 against emerald ash borer, for example (McCullough and Mercader, 2012). The program integrates the application of systemic insecticides, girdling and removing trees, and reducing phloem resources on the landscape via the removal of at-risk and infested host trees (Herms and McCullough, 2014). Indeed, host plant removal may be a useful technique in decreasing population growth and spread of emerald ash borer, despite social challenges and difficult logistics of removing and destroying large host plants (Suckling et al., 2012). Computer simulations have suggested, however, that host removal may exacerbate dispersal of emerald ash borers if individuals disperse farther to procure resources (Mercader et al., 2011b). Elucidation of the impacts of removing host trees on the population dynamics of emerald ash borer will bolster comparisons between management options and, potentially, aid decision-making by resource managers.

The aim of our study was to develop a simulation model from empirical data and apply it to determine if the removal of at-risk or infested trees in a recently-established satellite infestation of emerald ash borer could significantly influence population growth. In May 2009, emerald ash borer was discovered in Saint Paul, Minnesota, USA. The Minneapolis-Saint Paul region is an urban center of approximately 4 million people with the urban forest comprised of ~14% ash (> 11 million ash trees). Dendrochronological analyses showed a lag time of approximately 3–4 years between introduction and detection (N.W. Siegert, personal communication), and no trees were visibly dead at time of detection. After detection and an extensive delimitation survey, an aggressive tree removal program was undertaken in which trees with evidence of woodpecker foraging were targeted during annual removals. Log sections were sampled from standard areas of removed trees to characterize emerald ash borer populations. Specifically, larval densities and instar distribution were recorded, from which the proportion of the population emerging in the current *vs.* subsequent years was estimated.

Here, we analyze the effects of four years of host tree removal on the population growth of emerald ash borer from 2009 to 2013 in the Minneapolis-Saint Paul Metropolitan Area. We aimed to (1) quantify the effects of host tree removal on the cumulative number of beetles produced across four years, (2) determine if preferentially removing trees with woodpecking influenced cumulative beetle production, and (3) determine how voltinism may have moderated the efficacy of tree removal. Quantification of efficacy was achieved by comparing the actual management scenario to hypothetical management scenarios using a model parameterized with these data collected in Minnesota. We hope that conclusions from this study will improve decision making by municipalities and state governments in the management of newly-established satellite infestations of emerald ash borer as well as other invasive endophytic insect pests of trees.

2. Materials and methods

2.1. Core infested area

In 2009, the Minnesota Department of Agriculture (MDA) initiated a survey program throughout the Minneapolis-Saint Paul Metropolitan Area to delimit a recently established infestation of emerald ash borer. The delimitation survey used purple prism traps and external symptoms (e.g., evidence of woodpecker foraging, epicormics shoots, crown thinning) to identify trees that were potentially infested. A rhombus, the "core infested area," of approximately 6 km^2 was identified (Fig. 1). Ensuing management efforts between 2009 and 2013 were aimed at reducing emerald ash borer populations and phloem resources via the removal of ash trees. This study focused on 2370 ash trees in the core infested area at the start of our study in 2009. The primary goal of the study was to determine the impact of sanitation on emerald ash borer population growth. Consequently, we excluded 260 trees that were either treated with insecticides or girdled before removal during the course of the study because emerald ash borer numbers might be expected to be lower than average in treated trees and higher than average in girdled trees. Thus, there were 2370 ash trees in the core infested area at the start of our study in 2009 in addition to the 260 trees that had been subjected to girdling or treatment with insecticides. The *Fraxinus* component of the core infested area and removed trees were mostly *Fraxinus pennsylvanica* (Marshall) with a small portion of white ash *Fraxinus americana* (L.).

2.2. Tree surveys and removal

As part of ongoing surveys from 2009 to 2013 following the discovery of emerald ash borer in Saint Paul, the MDA recorded diameter at breast height (DBH; approximately 1.4 m above ground) and presence/absence of foraging damage by woodpeckers (referred to henceforth as "pecked or pecking"/"unpecked", respectively) on every tree in the core infested area. In emerald ash borer infestations, pecking appears relatively early compared to other symptoms such as epicormic shoots and thinning of the crown (Baranchikov et al., 2008; Lindell et al., 2008; McCullough and Mercader, 2012) and woodpecker predation is positively associated with densities of emerald ash borer (Lindell et al., 2008; Jennings et al., 2013, 2016). Thus, trees with pecking were targeted for removal. Surveyors were equipped with binoculars to increase detectability of pecking on branches in the upper crown. Surveys typically occurred during winter when leaves were absent and pecking was easier to detect.

Despite preferential removal of trees with pecking, both pecked and unpecked trees were removed during the study and removals occurred year-round (Table 1). For analyses, trees were assigned to a given removal year such that trees removed in Spring 2009 through Spring 2010 were recorded as removed in 2010, with similar patterns followed for 2011, 2012, and 2013. Over four years of removal, from 2010 to 2013, 1497 trees were removed (Table 1). In our data, 71 of the 2370

Fig. 1. Map of core infested area, Minneapolis-Saint Paul, MN, USA. Core infested area enclosed by a 6 km^2 polygon delimited via surveys by the Minnesota Department of Agriculture (MDA). First detection of emerald ash borer in Minnesota was near Hampden Park by an arborist in 2009, well before any tree mortality was observed.

Table 1
Summary statistics of the tree removal program by year from 2010 to 2013 in the core infested area in the Minneapolis-Saint Paul, MN, USA.

Status	Year	Trees	DBH (± SE) cm	Proportion pecked[a]
Removed	2010	197	31.8 (1.21)	0.87
Removed	2011	377	31.6 (0.84)	0.74
Removed	2012	641	18.1 (0.54)	0.32
Removed	2013	282	37.1 (1.06)	0.53
Removed	2010–2013	1497	26.7 (0.45)	0.54
Standing	2009	2370	27.6 (0.36)	
Standing	2014[b]	873	29.1 (0.59)	

[a] Proporotion of removed trees that had evidence of woodpecker foraging at time of removal. Thus, 13% of trees removed in 2010 did not have pecking.

[b] Reduction in trees was due to management. Most trees were removed preemptively and < 1% of trees were killed by emerald ash borer.

trees in the core infested area (3%) were missing DBH measurements. Ten of these trees were removed during management. Analyses required a measurement of tree size (see below), so each tree with a missing diameter record was assigned a randomly sampled value from a log-normal distribution fit to the values of diameters of all trees in the core infested area. This distribution was fit using maximum likelihood estimation (Fig. S1) via the fitdistrplus package in R (Delignette-Muller and Dutang, 2015). The maximum likelihood estimates for the log-normal distribution (± SE) were $\bar{x} = 3.14$ (0.01) and $s = 0.68$ (0.01).

2.3. Population growth

A population growth model for beetle production was developed to assess the efficacy of the management program implemented in the core infested area from 2010 to 2013. This model was built from empirical data and run for 200 simulations. Following is a detailed description of model construction and a summary is included in Table 2.

A portion of the trees removed between September and May were selected each year for subsampling to estimate the number of larvae per square meter of phloem in host trees. To determine larval densities, the bark was completely removed from a branch section or section of the main stem (i.e., a sample log). There were 894 sample logs ranging from 2.54–50.8 cm (mean = 12.6 cm) in diameter and 12.7–304.8 cm (mean = 90.6 cm) in length. The average diameter of a log, which are typically conical, was estimated by averaging the diameter measurements taken from both ends of the log. Number of logs sampled per tree ranged from 1 to 10 with a mean (± SE) of 3.43 (0.10) samples per tree. A total of 261 different trees were sampled. Larvae were recorded by developmental stage (i.e. instars one through four, j-larvae, and pre-pupae). Overwintering larvae in a j-shape were recorded as j-larvae whereas as all larvae that appeared straight, shortened, and broadened were recorded as pre-pupae (Wang et al., 2010). The total number per square meter of phloem was then calculated [= number of larvae in all stages/(average diameter of sample in meters × π × length of sample in meters)]. A summary of log sampling data and associated larvae are included in Tables 3 and 4, respectively. Log sampling data was aggregated to the tree level (i.e. total number of larvae found per total area of phloem examined per tree) such that each sampled tree had a single estimate for larval density. Given that presence/absence of pecking was recorded for each tree, the resulting data set of larval densities and trees was split into pecked and unpecked trees, producing two subsets of data. A linear mixed-effects model with a term for “sample year” fit as a random intercept was used to determine if the

Table 2
Summary of population growth model for larval emerald ash borers from 2010 to 2014 in the core infested area in Minneapolis-Saint Paul, MN, USA with statistical distribution and parameters.

Step	Procedure
1.	If tree does not have a recorded diameter, randomly assign a value from a log-normal distribution ($\bar{x}$ = 3.14 cm, s = 0.68 cm)
2.	Estimate surface area of each tree based on its diameter at breast height (Eqs. (2) and (3) in text).
3.	Define the carrying capacity for larvae per square meter of phloem for each tree.
4a.	If a tree is pecked, determine if that tree will contain larvae using a random sample from a binomial distribution (p = 0.82). If the draw is equal to 1, randomly draw a value for larval density from a log-normal distribution ($\bar{x}$ = 1.70 larvae per square meter of phloem, s = 1.05). If the draw is equal to 0, then the tree will not contain larvae.
4b.	If a tree is not pecked, determine if that tree will contain larvae using a random sample from a binomial distribution (p = 0.53). If the draw is equal to 1, randomly draw a value for larval density from a log-normal distribution ($\bar{x}$ = 0.59 larvae per square meter of phloem, s = 0.90). If the draw is equal to 0, then the tree will not contain larvae.
5.	Scale the number of larvae per square meter of phloem to the number of larvae per surface area of the entire tree. These larval densities equal the estimated beetle population emerging in spring 2010 (year 1).
6.	Take a random draw to obtain a simulation-specific growth rate, Gaussian($\bar{x}$ = 1.90, s = 1.01).
7.	Grow beetles produced by each tree for "3–X" steps, where X = the number of years before 2013 that a tree was removed. That is, trees removed in 2010 would be grown for 3-3 = 0 time steps, as these trees would be removed before beetles could emerge from them in spring 2010. For the *no removal* scenario, X = 0 for each year. For scenarios with mixed voltinism, number of adults emerging from a given pecked tree or unpecked trees was multiplied by 0.61 and 0.42, respectively. The remaining proportions (0.39 and 0.58) emerged the following year if the tree was not removed.
8.	Record yearly number of beetles produced for each year in each management scenario.
9.	Repeat steps 1–8 for 200 iterations. An additional 600 simulations were run, 200 with R ~ Gaussian($\bar{x}$ = 5.18, s = 1.51), 200 with R ~ Gaussian($\bar{x}$ = 10.35, s = 3.02), and 200 with R ~ Gaussian($\bar{x}$ = 10.35, s = 0)

larvae per square meter of phloem differed between pecked and unpecked trees (α = 0.05). The variable for larval density was log-transformed ($\log_e(y + 0.01)$) to meet assumptions of homoscedasticity of the errors.

To run simulations, every tree in the data set required a value for larval density in 2010 (at the start of management). For trees that were directly sampled, we calculated larval densities in 2010 as follows:

$$N_{1,i} = \frac{N_{y,i}}{R^{y-1}} \tag{1}$$

where $N_{1,i}$ is the number of larvae per square meter of phloem in tree i in year 1 (2011), $N_{y,i}$ is the number of larvae per square meter of phloem in tree i in year y, and R is the population growth rate. Thus, if a tree was directly sampled, that empirical estimate for larval density was used. The growth rate, R, was the same for each tree within a simulation and was randomly drawn from a Gaussian distribution with $\bar{x}$ = 1.90 and s = 1.01 at the start of each simulation. The mean and standard deviation of the statistical distribution were calculated from the 3 ratios of larvae per square meter of phloem in unpecked trees in successive years (e.g., 2012 larval density/2011 larval density in unpecked trees = 1.42, 2013/2012 = 3.05, and 2014/2013 = 1.21). Ratios of larval densities across years were used to obtain a growth rate applicable to the satellite infestation under investigation. The growth rates we estimated were within but on the lower end of growth rates reported in the primary literature (Mercader et al., 2011a; Duan et al., 2014, 2015). The growth rate was sampled at the start of each simulation. Larval densities for each year (2010–2013) were necessary to estimate the number of beetles emerging from each tree in each year.

We used our empirical data to estimate larval densities in trees that were not directly sampled. Using all trees that were removed in 2011, the proportion of both pecked and unpecked trees containing emerald ash borer was quantified (p = 0.82 for pecked trees and p = 0.53 for unpecked trees). For trees that were positive for emerald ash borer, a log-normal distribution was fit to the larval density of both pecked and unpecked trees using maximum likelihood estimation via the fitdistrplus package in R (Delignette-Muller and Dutang, 2015). The maximum likelihood estimates for the mean (± SE) and standard deviation (± SE), respectively, were 1.70 (0.13) and 1.05 (0.09) larvae per square meter of phloem for pecked trees compared to 0.59 (0.32) and 0.90 (0.22) for unpecked trees (Fig. S1). Each tree that was not sampled directly was then assigned a larval density (larvae/m^2 phloem) based on two random draws from either pecked-specific or unpecked-specific

Table 4
Summary of larval data from sample logs taken from trees removed between 2010 and 2013 in the core infested area in Minneapolis-Saint Paul, MN, USA. Data were used to estimate number of larvae requiring an extra year to complete development.

Year	Larvae detected	Proportion in pecked samples[a]	Proportion of larvae expected to emerge in current year from pecked samples[b]	Proportion of larvae expected to emerge in current-year from unpecked samples[b]
2010	706	0.62	0.65	0.25
2011	752	0.64	0.58	0.55
2012	97	0.67	0.55	0.47
2013	52	0.67	0.69	0.88

[a] Proportion of larvae within a given year that were found in a pecked log sample.
[b] Current-year larvae = larvae in the 4th instar or any subsequent immature stage. Current-year larvae are expected to emerge within 1 year from time of observation.

Table 3
Summary of 894 log samples aggregated to the tree level for trees removed from 2010 to 2013 in the core infested area in Minneapolis-Saint Paul, MN, USA.

Year	Trees sampled	Proportion pecked	Proportion infested[a]		EAB density[b] (± SE)	
			Pecked	Unpecked	Pecked	Unpecked
2010	91	0.87	0.82	0.53	7.52 (1.13)	1.36 (0.52)
2011	139	0.74	0.70	0.44	5.77 (0.81)	2.62 (0.99)
2012	16	0.32	0.78	0.57	6.20 (1.68)	5.92 (2.59)
2013	12	0.53	0.43	0.60	10.9 (9.10)	3.57 (2.02)
Total	258	0.54	0.74	0.49	6.65 (0.69)	2.76 (0.67)

[a] Values do not sum to 1, as proportions reported refer to the percent of pecked and unpecked trees that contained larvae, respectively (e.g., 82% of trees with pecking in 2010 were infested compared to unpecked trees in 2010 of which only 53% were infested).
[b] Larvae per square meter of phloem.

Table 5
Definitions for the tree removal scenarios that were simulated for the core infested area in Minneapolis-Saint Paul, MN, USA.

Management scenario[a]	Type of scenario	Description
Actual	Actual	Actual management scenario for core infested area in which trees were selectively removed from the landscape.
No removal	Hypothetical	No trees removed from the core infested area.
Delayed	Hypothetical	Removed same number of trees as *actual*, except all removals occurred at a single time point in winter 2013.
Pecked-only	Hypothetical	Removed only the pecked trees out of trees removed under *actual*.
Random	Hypothetical	Removed same number of trees per year as *actual*, except removals were done randomly.
Adjusted-random	Hypothetical	Removed same trees as *random*, except trees were standardized for surface area so that phloem removed was equivalent to *actual*.
Voltinism	Actual	Equivalent to *actual* except accounted for delayed beetle emergence between pecked and unpecked trees
No removal-voltinism	Hypothetical	Equivalent to *no removal* except accounted for delayed beetle emergence between pecked and unpecked trees

[a] All emerald ash borer populations were assumed to be univoltine for all management scenarios except for *voltinism* and *no removal-voltinism*, in which a proportion of the populations were assumed to require an extra year to complete development.

distributions. The first draw was from a binomial distribution and, if the draw was equal to 1 (indicating presence of emerald ash borer), a second draw from a log-normal distribution was assigned as the larval density. For pecked and unpecked trees, the binomial distributions were parameterized with $p = 0.82$ and $p = 0.53$ whereas the log-normal distributions were parametrized with $\bar{x} = 1.70$ and $s = 1.05$ and $\bar{x} = 0.59$ and $s = 0.90$, respectively. Thus, every tree in the data set that was not directly sampled was randomly assigned a larval density based on statistical distributions parameterized using data collected in 2011 from pecked and unpecked trees in the core infested area.

Each tree in the data set was also assigned a carrying capacity for larvae per square meter of phloem. The carrying capacity of larvae per tree, K, was randomly assigned based on published estimates of maximum number of exit holes per square meter of phloem: 105 (± 5.7 SE) estimated from 39 large trees (> 13 cm in DBH) and 69 (± 5.9 SE) estimated from 32 small trees (≤13 cm in DBH) (McCullough and Siegert, 2007). To permit variation in maximum beetle production per square meter of phloem, two Gaussian distributions were parameterized with $\bar{x} = 105$ and $s = (5.7\times)$ for large trees and $\bar{x} = 69$ and $s = (5.9\times)$ for small trees. The larval density per square meter of phloem for each tree was capped at this randomly assigned carrying capacity to protect against randomly assigning impossibly high larval densities.

Larval densities were then scaled from larvae per square meter of phloem to larvae residing in the entire tree. To achieve this, the surface area of trees (i.e. amount of phloem available to developing larvae) was estimated using two regression equations published by McCullough and Siegert (2007) that relate diameter at breast height to surface area for ash trees. Using data from green ash (*F. pennsylvanica*) and white ash (*F. americana*) trees, McCullough and Siegert (2007) developed separate equations for large trees (> 13 cm in DBH; Eq. (2)) and small trees (≤13 cm in DBH; Eq. (3)):

$$phloem_i = 2.630(\pm 0.881) - dbh_i \times 0.307(\pm 0.081) + dbh_i^2 \times 0.024(\pm 0.001) \tag{2}$$

$$phloem_i = -1.759(\pm 0.274) + dbh_i \times 0.380(\pm 0.027) \tag{3}$$

where $phloem_i$ is the amount of suitable phloem for emerald ash borer development in tree i and dbh_i is the diameter (cm) at breast height of tree i. Numbers in parentheses are standard errors of regression coefficients. For each tree, regression coefficients were randomly drawn from a Gaussian distribution with means and variances equal to slope coefficients and standard errors. On rare occasions where a random draw resulted in a negative number, the value was resampled.

The estimates of phloem area and larvae per square meter of phloem were multiplied to obtain the number of larvae in each tree in fall 2009 (before the first removal). For simplicity and given the relatively low densities of larvae per square meter of phloem observed in our empirical data (max = 65.03, mean = 5.73, SE = 0.56) relative to expected carrying capacities for a square meter of phloem (Herms and McCullough, 2014), all larvae were assumed to emerge if the host tree was not removed. This procedure resulted in a cohort of emerged beetles per tree in spring 2010 that was propagated for three time steps (2010–2013) on a per tree basis according to the following discrete time model:

$$N_{t,i} = N_{t-1,i} - R \tag{4}$$

where $N_{t,i}$ is the number of beetles produced by tree i in year t, $N_{t-1,i}$ is the number of beetles produced by tree i in the previous year, and R is the population growth rate.

Model progression began with a bout of tree removal followed by beetle emergence. The number of beetles emerging each year was stored to enable calculation of cumulative emergence by spring 2013. The growth rate was defined as in Eq. (1). We elected to use a model without a carrying capacity for total beetles produced on the landscape because we are interested in estimating beetle pressure, or the total number of beetles resulting (not necessarily emerging) from each tree per year. Therefore, the model included beetles produced by a tree that potentially dispersed to and reproduced in another tree the following year. This assumes that, during our four-year study, emerald ash borer did not consume all available phloem resources, which we deemed appropriate as trees in the surrounding area were not exhibiting mortality as of 2015. All steps involving randomization were simulated anew for each iteration of the model.

2.4. Management scenarios

Cumulative number of beetles produced across four years was estimated for eight different management scenarios in which trees were or were not removed. A summary of each removal scenario is provided in Table 5. The *actual* scenario represented the actual tree removal program whereas *no removal* represented a scenario in which no trees were removed from the core infested area. In the *delayed* scenario, the same trees were removed as under the *actual* removal scenario except that tree removal occurred at a single time point in winter 2013, the last year of the study. The *delayed* scenario was used to quantify the benefits of early detection and removal compared to a significant time lag between establishment and detection. Under the scenario *pecked-only*, the same trees were targeted for removal as under the *actual* scenario except that trees without pecking were left standing. Under the *random* scenario, the same numbers of trees were removed per year as *actual* but removals were done randomly. Thus, the trees that were removed could have been removed during the actual management, or may still be present in the core infested area. The *adjusted-random* scenario was equivalent to *random* scenario except that the surface area of trees in *adjusted-random* were randomly sampled, without replacement, from the *actual* scenario trees to account for differences in phloem resources between removals. The *adjusted-random* scenario was included to quantify the benefits of targeting pecked trees while holding phloem resources constant.

The *actual, no removal*, *delayed*, *pecked-only*, *random*, and *adjusted-random* scenarios assumed that beetle populations were completely univoltine. However, it is well documented that populations of emerald ash borer developing in the same tree can develop through either a semivoltine or univoltine life cycle (Wei et al., 2007; Tluczek et al., 2011). If pecked trees have higher proportions of larvae that complete development in a single year compared to unpecked trees, then preferentially removing them may increase efficacy as an extra year could be afforded to managers to remove the unpecked trees with higher proportions of larvae with delayed emergence. We use the terms "current-year larvae" and "delayed larvae" instead of univoltine and semivoltine, as 4th instar larvae may be semivoltine individuals but in their second year of development. Current-year larvae refer to insects that are expected to emerge in the following spring, whereas delayed larvae refers to insects expected to emerge a year from the following spring. To estimate if the probability of an individual emerging the following spring was associated with pecking, we classified all larvae found during empirical sampling in instars one through three as "delayed larvae" and otherwise as "current-year larvae." We tested whether the probability of current-year emergence was associated with woodpecking status of the sample using a generalized linear mixed-effects model with random intercepts for tree and log nested within tree. A binomial error structure and logit link were used. After concluding that emergence was more likely to occur in the present year from pecked logs (see Results), the additional selective removal scenario, *voltinism*, and associated no management scenario, *no removal-voltinism*, were simulated. In both scenarios, a proportion of the insects within each tree were assumed to require two years to complete development. The proportion of current-year larvae observed in log samples was 61% and 42% in pecked and unpecked samples, respectively. We incorporated delayed emergence into the model by multiplying the number of emerging beetles per year in either pecked or unpecked logs by the proportion that are current-year larvae (i.e. 0.61 for beetles emerging from pecked tress, 0.42 for beetles emerging from unpecked trees). The remaining proportion of beetles (i.e., delayed larvae) would emerge the following year if their host tree was not removed. The *voltinism* scenario resulted in the removal of the same exact trees as removed under *actual* above.

For each scenario, beetle production was estimated for each year and the model was run for 200 simulations, totaling 1600 simulations and 6400 values of beetle production. That is, a value was recorded for each year (2010–2013) in each scenario (8) and for each simulation (200). To quantify efficacy, we compared cumulative beetle production under the actual removal program with univoltine development (*actual)* to the other management scenarios that assumed completely univoltine populations (*no removal*, *delayed*, *pecked-only*, *random*, and *adjusted-random*). Next, to understand the importance of voltinism in beetle production and management efficacy, the *voltinism* scenario was compared to *no removal* and *no removal-voltinism.* In addition to comparisons after four years of management, a comparison between *actual* and *no removal* within each year of management was conducted to compare temporal patterns in efficacy.

2.5. Sensitivity analyses

To test sensitivity of our results to population growth rates, we ran 1200 additional simulations using three different distributions of growth rates. For each of the *actual* and *no removal* scenarios, 200 simulations were ran with *R* sampled from a Gaussian distribution with $\bar{x} = 5.18$ and $s = 1.51$, $\bar{x} = 10.35$ and $s = 3.02$, and $\bar{x} = 10.35$ and $s = 0$. The first two distributions were used to evaluate how efficacy shifted with changes in mean growth rate whereas as the third distribution was used to evaluate how efficacy shifted with variance in growth rate. These growth rates reflect published growth rates of emerald ash borer in other regions of the United States (Mercader et al., 2011a; Duan et al., 2014, 2015). Percent reduction in beetle production when implementing the *actual vs. no removal* scenario was calculated after 4 years for each distribution of *R*, producing 600 values.

2.6. Statistical analyses

Formal statistical comparisons between management scenarios were conducted by calculating the percent reduction in cumulative beetle production at the end of each year in each simulation as follows:

$$\%\text{reduction}_t = \left(1 - \frac{\text{scenario}_{i,t}}{\text{scenario}_{r,t}}\right) \times 100 \tag{5}$$

where *% reduction* is the reduction in cumulative number of beetles produced after *t* years of management as a result of removing trees via $scenario_i$ compared to $scenario_r$, $scenario_i$ is the number of beetles produced in scenario *i* after *t* years of management, and $scenario_r$ is the number of beetles produced in the reference scenario after *t* years of management. Management scenarios were considered statistically different if the 95% confidence interval for percent reduction in larvae (i.e. the middle 95% of simulation values) excluded zero. We conducted yearly comparisons of the *no removal* scenario ($scenario_r$ in Eq. (5)) to *actual*, *random*, and *pecked-only* scenarios ($scenario_{i=1,2,3}$ in Eq. (5)) to determine if the relationship between percent reduction in cumulative number of beetles produced and cumulative percent of trees removed changed across time. Otherwise, all comparisons between management programs were conducted for cumulative beetle production cross all four years ($t = 4$). All analyses were completed using R (R Core Team, 2016). All mixed-effects models were fit using the lme4 package (Bates et al., 2013) and *P*-values were obtained using Satterthwaite's approximation for the degrees of freedom via the lmerTest package (Kuznetsova et al., 2014).

3. Results

Removing trees with evidence of woodpecker foraging significantly decreased the cumulative number of emerald ash borer adults produced in the core infested area across four years of management. Trees with pecking had an average of 2.4 more larvae per square meter of phloem, significantly more than unpecked trees ($F_{1,255} = 17.28$, $P < 0.0001$). Under the *actual* scenario, the median cumulative number of adults produced in the core infested area was 1.6 million (M) (95% CI: 0.6–5.8; Fig. 2A) compared with 3.4 M adults that would have been produced if no trees had been removed (95% CI: 1.1–13.9; *no removal* scenario in Fig. 2B). Under *delayed* removal, cumulative beetle production was 2.2 M (95% CI: 0.9–7.4; Fig. 2C). Under a *pecked-only* scenario, where only pecked trees within the *actual* scenario were removed (reducing percent of trees removed from 63.2% to 33.8%), a median of 1.7 M (95% CI: 0.6–6.5; Fig. 2D) adults were produced in the core infested area across four years of management. Thus, focusing on removal of trees with woodpecker damage allowed removal of approximately half as many trees as the actual management strategy undertaken, while resulting in only slightly greater beetle production.

Under a *random* removal scenario, the median estimated number of beetles produced in the core infested area was 1.6 M (95% CI: 0.6–6.1; Fig. 2E). Under an *adjusted-random* scenario, in which randomly removed trees were adjusted for surface area to match the *actual* scenario, there was a median of 1.7 M (95% CI: 0.6–6.4; Fig. 2F) beetles produced in the core infested area. The adjustment for surface area resulted in more larvae on the landscape because the trees removed under selective management were smaller by 4.4 cm on average compared to trees left standing ($t = 6.16$, df = 1786, $P < 0.0001$). Thus, the *random* scenario resulted in an increased probability of removing a larger tree than those removed under the *actual* scenario. Under the *voltinism* scenario, in which delayed emergence was included in the model and the same number of trees were removed as in the *actual* scenario, cumulative beetle production was 1.2 M (95% CI: 0.5–3.9; Fig. 2G). Under the *no removal-voltinism* scenario, cumulative beetle production was much higher than the *voltinism* scenario at 2.6 M beetles (95% CI: 0.9–9.6; Fig. 2H).

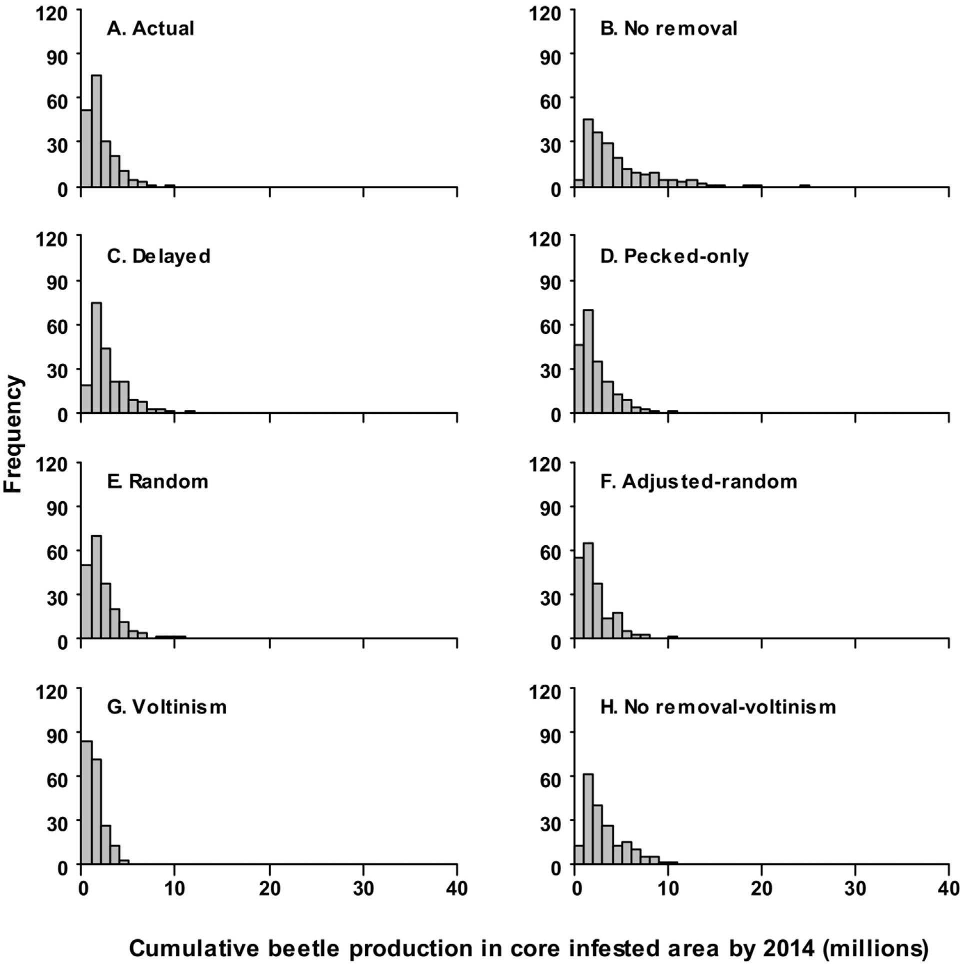

Fig. 2. Estimates of cumulative number of beetles produced in the core infested area across four years of tree removal programs in the core infested area in Minneapolis-Saint Paul, MN, USA. See Table 5 for explanation of removal scenarios.

Each of the hypothetical removal scenarios that assumed beetle populations were univoltine was then compared to the *actual* scenario (i.e., *actual* was set to $scenario_i$and each hypothetical scenario was set to $scenario_r$ in Eq. (5)) (Fig. 3). If there was a positive difference between scenarios and the 95% confidence interval did not include “0”, this provided strong evidence that the *actual* management scheme was superior to the scenario under comparison in terms of reducing cumulative beetle production. The percent reduction in cumulative beetle production under *actual* compared to *no removal* was significant, as removing 63.2% of the total trees across four years reduced beetle numbers by a median of 54.1% (95% CI: 42.4–61.2%; Figs. 3A, 4C) in the core infested area. Moving from *delayed* to *actual* removal highlighted the importance of early detection and management, as beetle production was reduced by 27.1% (95% CI: 20.2–32.8%; Fig. 3B) across four years. A change to *actual* removal from *pecked-only*, in which 33.8% of the trees were removed from the core infested area, resulted in an estimated median reduction of 8.6% of insects (95% CI: 5.7–12.9%; Fig. 3C) after four years. Targeting pecked trees appeared to be slightly more advantageous than simply removing the same number of trees at random, as a change from *random* to *actual* reduced the number of larvae after four years by an additional 4.4% (95% CI: −11.0–16.7%; Fig. 3D). This finding did not appear to be moderated by the fact that trees removed under the *actual* scenario were smaller by an average of 4.4 cm than trees left standing, as a change to *actual* from *adjusted-random* resulted in a 3.0% (95% CI: −22.1–23.5%; Fig. 3E) reduction in beetles produced.

Accounting for extended development in a fraction of the population appeared to have merit, as pecked branch samples contained higher proportions of current-year larvae on average. For example, if sampling from a pecked versus unpecked branch, the odds of finding a current-year larva increase by 2.49 ($Z = 4.11$, $P < 0.0001$). Simulations using delayed emergence suggested that, in addition to removing more larvae per square meter of phloem, targeting pecked trees removed higher proportions of current-year larvae and afforded managers an extra year to remove the delayed larvae. Comparing *voltinism* to *no removal-voltinism* resulted in an estimated percent change in cumulative beetle reduction of 55.4% (95% CI: 44.7–62.3%; Fig. 4A). When *voltinism* was compared to *no removal* (i.e. completely univoltine populations), cumulative beetle production was decreased by 63.6% (95% CI: 50.3–71.5%; Fig. 4B).

Comparisons across years between *actual* and *no removal* suggest that, across the first four years of tree removal, a selective removal program can delay population growth by 1–2 years (Fig. 5). Annual comparisons of *actual*, *random*, and *pecked-only* scenarios to *no removal* demonstrated that a drop in efficacy occurred in 2012 (year 3 of management) due to a change in tree removal strategy (Fig. 6). In this year, a large number of relatively small trees were removed from a wooded park in an effort to manage towards non-ash species. Indeed, there were 641 trees removed in 2012, or 1.7 times the next highest number. Trees removed in 2012 had a mean DBH of 18 cm, more than 13 cm smaller on average than the next smallest cohort of removed trees. Moreover, a smaller percent (32%) of the trees were pecked, compared to the next smallest percentage of 53% observed in 2013 (Table 1). We compared the ratio of median percent reduction in cumulative beetle production to cumulative percent tree removal. A ratio greater than 1 suggests that removal of trees had a dispropor-

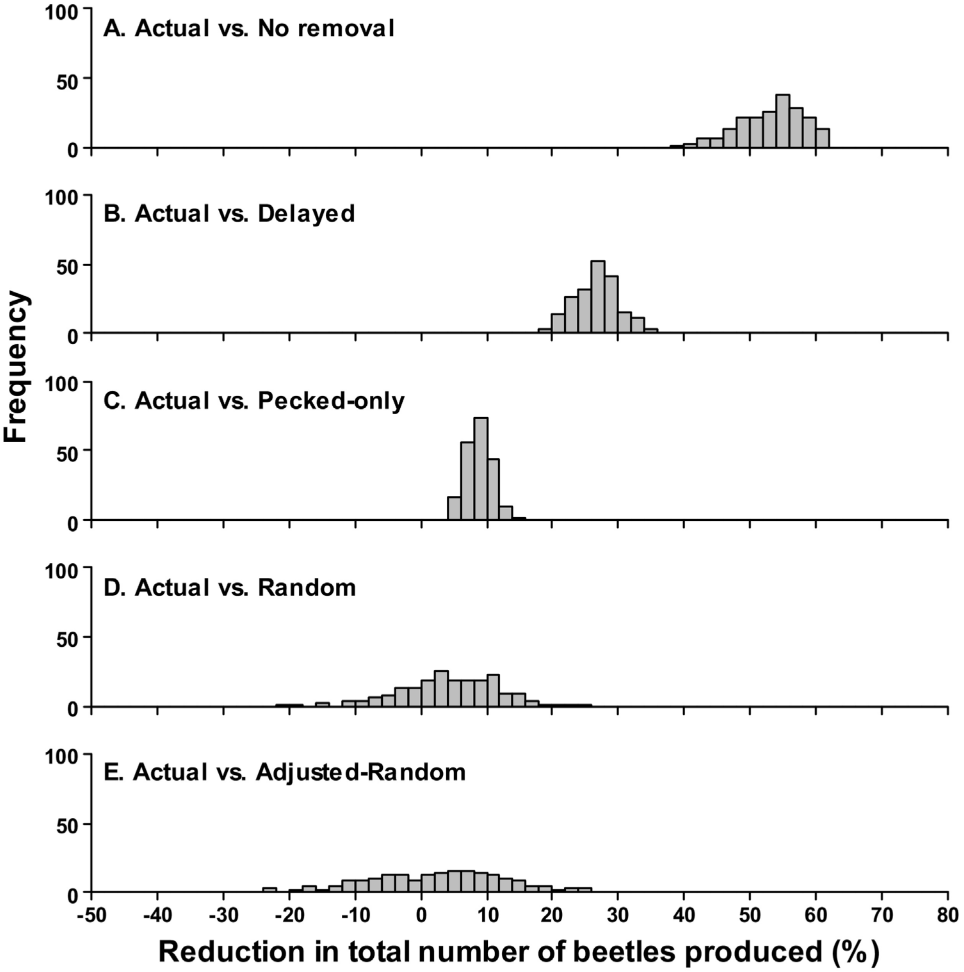

Fig. 3. Percent reduction in cumulative number of beetles produced after four years (2010–2013) of tree removal in the core infested area in Minneapolis-Saint Paul, MN, USA. Negative numbers indicate that there would have been more insects resulting than under the removal regime pursued.

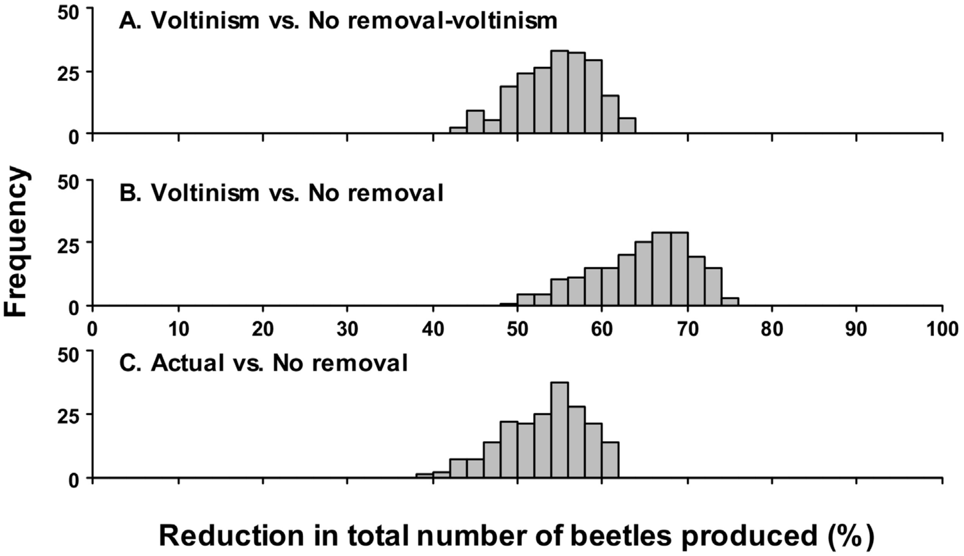

Fig. 4. Percent reduction in cumulative number of beetles produced after four years (2010–2013) of tree removal in the core infested area in Minneapolis-Saint Paul, MN, USA. Figure shows comparisons of A) *voltinism* to *no removal-voltinism* (i.e., both scenarios with mixed voltinism) and B) *voltinism* (mixed voltinism) to *no removal* (completely univoltine) C) *actual* to *no removal* (i.e., both scenarios with completely univoltine populations). Panel C is similar to Fig. 3A but reproduced here for ease of comparison.

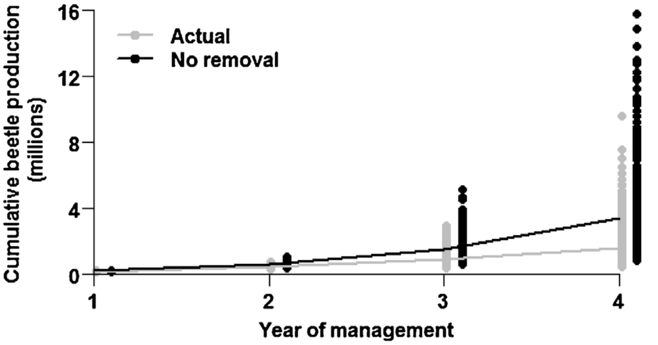

Fig. 5. Cumulative beetle production under *actual* versus *no removal* scenarios across four years (2010–2013) of management in Minneapolis-Saint Paul, MN, USA.

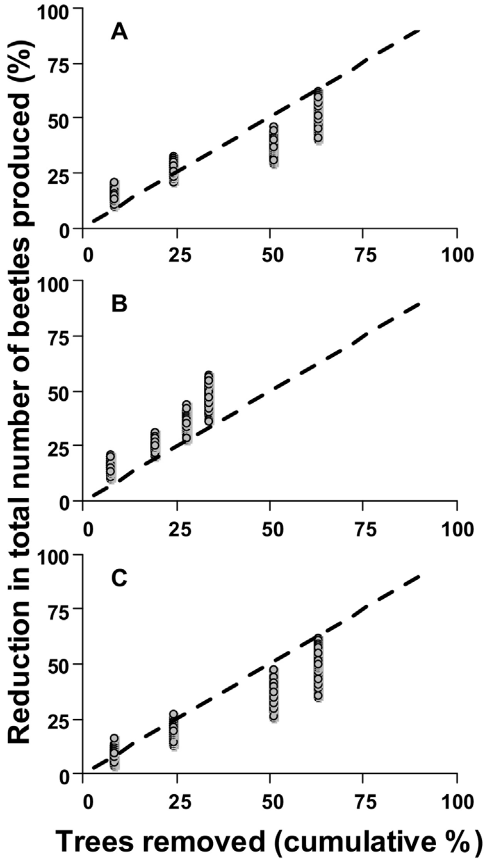

Fig. 6. Efficacy of A) *actual* B) *pecked-only* and C) *random* scenarios versus *no removal* across four years (2010–2013) of management in Minneapolis-Saint Paul, MN, USA. Figure shows association of percent reduction in cumulative beetle production with cumulative percentage of trees removed. Each dot represents within-year values for a single simulation. A ratio greater than 1 (i.e. a point above the dashed line) suggests that removal of a percentage of the trees had a disproportionate, advantageous impact on the reduction of beetles (i.e. greater percentage reduction).

tionate, advantageous impact on the reduction of beetles (e.g., removal of 5% of trees resulted in > 5% reduction in beetles). This ratio was greater than one until year 3 for the *actual* scenario (1.89, 1.12, 0.75, and 0.86; Fig. 6A). Under the *pecked-only* scenario all years had a ratio greater than 1 (2.15, 1.37, 1.33 and 1.46; Fig. 6B) compared to the *random* scenario under which no year had a ratio greater than 1 (0.99, 0.79, 0.74, and 0.82; Fig. 6C).

Sensitivity analyses suggested that reductions in population growth increased with mean growth rate until R reached approximately 5, at which point efficacy plateaued (Fig. 7A). Comparisons between percent reduction between the *actual* and *no removal* scenarios where growth rate was allowed to vary in one scenario ($R = 10.35 \pm 3.02$ SD) but held constant in another ($R = 10.35$) demonstrated that estimates of percent reduction were not heavily influenced by variance in growth rates (Fig. 7B).

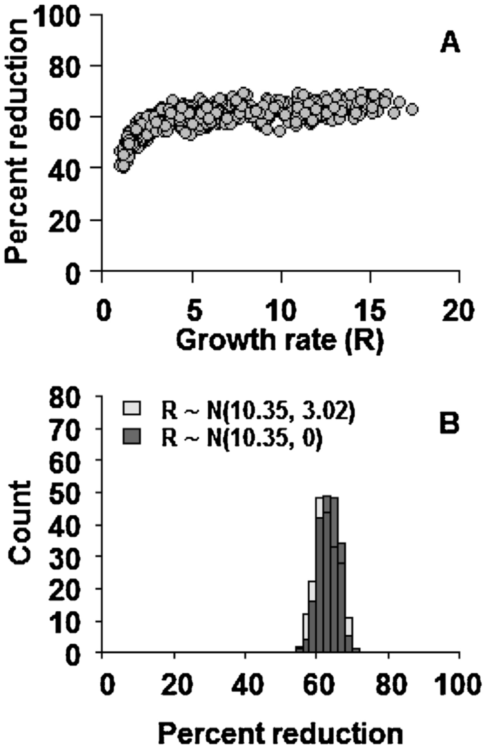

Fig. 7. Sensitivity analysis depicting the effect of growth rates on percent reduction of beetles due to *actual* removal scenario in the core infested area in Minneapolis-Saint Paul, MN, USA. Figure depicts effects of A) mean growth rate on percent reduction and B) variance in growth rates on percent reduction.

4. Discussion

Our results demonstrate that aggressive sanitation of a satellite population of emerald ash borer, if detected early, can slow population increase by approximately 54% versus doing nothing. The suppression was achieved by preferentially removing ash trees with evidence of woodpecker feeding from within the satellite infestation across four years. These results are likely conservative, as our sampling methods may have overestimated the densities of emerald ash borer in unpecked trees. Unpecked trees that were sampled were generally in close proximity to pecked trees and more likely to be infested than unpecked trees in other parts of the core infested area. The effectiveness of concentrating on pecked trees was clear, as the total number of beetles produced in the *pecked-only* scenario (1.7 M) was comparable to the *actual* scenario (1.6 M) but only 34% of the trees were removed in the *pecked-only* simulation compared to 63% in *actual*.

The eradication of emerald ash borer is not a feasible management goal even in satellite infestations, although tree removal within a few years following establishment (before mortality becomes apparent) can result in up to a two-year delay in population growth (Fig. 5). Given the rapid rate at which almost complete mortality of the mature ash component can occur following infestation of emerald ash borer (e.g., 99% in less than 6 years in forested areas; Knight et al., 2013), a two-year delay will benefit managers by increasing time for the implementation of other management strategies. Prior simulation studies have found that treating trees with stem injections of emamectin benzoate or using girdled trees as population sinks rank among the most effective management options to reduce population growth, for example (Mercader et al., 2011a,b; McCullough and Mercader, 2012; McCullough et al., 2015). We expect that girdling and removing trees enhanced emerald ash borer control efforts in the Twin Cities metropolitan area, although we do not believe that excluding the 260 treated/girdled trees from the present analyses accentuated our conclusions as the sensitivity analyses were robust to variability in growth rates (Fig. 7).

The strategy of proactively removing ash in advance of emerald ash borer arrival to slow the ultimate mortality of ash, which lacks empirical support (Knight et al., 2013; Smith et al., 2015), is distinct from our emphasis to remove infested trees to reduce the number of insects and "buy time." Systematic replacements of ash trees in urban areas or ash-dominated forest stands do accomplish important goals of diversification and buffering impacts on ecosystem function (Iverson et al., 2016). Resource managers should interface budgetary constraints and geographic extent and severity of the infestation with current and future goals as they pertain to the composition of the urban forest. Management efforts and goals should be employed and developed, respectively, on a site-specific basis and select from the several integrated pest management techniques that have been developed to date to combat this pest (Vannatta et al., 2012; Kovacs et al., 2014; Herms and McCullough, 2014; Sadof et al., 2017).

In some instances, guidelines are still developing. To guide decision-making by land managers and private property owners regarding when a tree should be removed versus treated with insecticides, for example, a relationship between larval density and efficacy of insecticides is necessary. Given the difficult logistics of sampling trees directly to obtain an estimate of larval density, crown ratings are often used as a proxy for both larval density (Flower et al., 2013) and the potential efficacy of emamectin benzoate (Flower et al., 2015). Thus, deciding whether or not to remove a tree should depend on that tree's expected lifespan following application of an insecticide, balancing the percent of phloem remaining with the tree's monetary, aesthetic, and cultural values. Indeed, in simulations by McCullough and Mercader (2012), trees were only considered for removal when greater than 60% of the phloem was consumed.

Our results show that a two-year life cycle for emerald ash borer can afford managers an extra year to treat or remove trees and results in a decrease in cumulative beetle production. Comparisons of *voltinism* to *no removal* scenarios suggest that significant increases in percent reduction of ~64% may occur if removing trees helps maintain the proportion of the population that requires an extra year to complete development. Warmer climates and stressed trees are predicted to have higher proportions of univoltine (current-year) beetles (Wei et al., 2007; Tluczek et al., 2011). The failure to remove trees will increase beetle production and lead to additional weakened trees on the landscape in the early stages of an infestation. If more stressed trees increases the proportion of the population that is univoltine, then the benefits of removing trees could be compounded. The *voltinism* to *no removal* comparison may be considered an extreme case in which, under no management, all insects are univoltine.

In examining the beetle production through time, it was clear that a marked decrease in efficacy was associated with the removal of trees in 2012 (year 3 of management; Fig. 6A). The decrease in efficacy was likely driven by the removal of smaller trees on average and the decrease in the proportion of removed trees that had pecking for 2012 (Table 1). In comparing temporal trends of *actual* to *pecked-only* scenarios, it was clear that higher percent reductions per tree were achieved by targeted removal, despite that greater absolute percent reductions were achieved by simply removing more trees.

It is difficult to empirically determine whether tree removal could affect spread, especially in situations where new introductions may occur with high frequency. Simulation studies have suggested that host tree removal may lead to an increase in dispersal distances by emerald ash borer as emerging beetles search for oviposition sites on a landscape depleted of ash by management efforts (Mercader et al., 2011a,b). Studies of tethered flight show that emerald ash borer can fly several kilometers (Taylor et al., 2010; Fahrner et al., 2015). Indeed, during initial attempts to prevent the spread of emerald ash borer in Essex County, Ontario, Canada, the beetle likely dispersed across a 10 km wide buffer zone from which all ash trees had been removed (Taylor et al., 2010). Given the flight and dispersal capacity of emerald ash borer, and the response of dispersal by emerald ash borer to phloem resources (Siegert et al., 2010), it is almost certain that emerald ash borer spread beyond the core infested area during this study. Yet, despite these projected dispersal patterns, several trees remain in the core infested area and appear healthy.

Another potentially important factor in the management of emerald ash borer are Allee effects in population growth and spread (Liebhold and Tobin, 2008; Tobin et al., 2011). A positive correlation between spread rates and initial population density of emerald ash borer were found in cellular automata models developed by Mercader et al. (2011b), for example. Estimates for growth and spread of populations of emerald ash borer that account for potential challenges in mate finding in low density infestations, however, have not yet been achieved (Mercader et al., 2011a,b). Studies on European gypsy moth *Lymantria dispar dispar* (L.) (Lepidoptera: Erebidae), for example, show that reduction of gypsy moth populations to low densities leads to decreases in mate finding ability and thus slower population growth and expansion (Johnson et al., 2006; Tobin et al., 2007 Tobin et al., 2007). Models of spread that incorporate Allee effects will improve predictions of the role of dispersion of phloem resources, both in managed and un-managed landscapes, in population growth and spread of emerald ash borer.

Our study demonstrates the importance of efficient and early detection as well as the potential roles of regional differences in population density, growth rates, and voltinism in managing endophytic herbivores via host tree removal. As an endophytic herbivore with no identified long-distance sex pheromone (Herms and McCullough, 2014) and the presence of a long lag time between infestation and easily-detectable tree symptoms (Cappaert et al., 2005), emerald ash borer remains a challenging invader to manage (Herms and McCullough, 2014). Following the early discovery of a satellite infestation of emerald ash borer in an urban area, tree removal may be a useful management tool to reduce populations of emerald ash borer as part of a broader, integrated pest management program. Larger diameter trees with pecking will likely contain the most larvae (McCullough and Siegert, 2007; Lindell et al., 2008; Jennings et al., 2013, 2016). Within tree removal strategies, preferentially removing large trees will be most effective in reducing beetle production.

Acknowledgements

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Appendix A. Supplementary material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ufug.2017.03.017.

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