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Reproduction and Control of the Invasive Polyphagous Shot Hole Borer, *Euwallacea* nr. *fornicatus* (Coleoptera: Curculionidae: Scolytinae), in Three Species of Hardwoods: Effective Sanitation Through Felling and Chipping

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Abstract

The invasive ambrosia beetle polyphagous shot hole borer is one member of the cryptic species, *Euwallacea* nr. *fornicatus* (Eichhoff), and poses a great ecological and environmental threat to ornamental and native hardwood trees and agriculturally important tree crops in southern California, United States. We monitored the emergence of polyphagous shot hole borer adults from chipped and unchipped cut logs of infested boxelder, *Acer negundo* L. (Sapindales: Sapindaceae), California sycamore, *Platanus racemosa* Nutt. (Proteales: Platanaceae), coast live oak, *Quercus agrifolia* Née (Fagales: Fagaceae), and red willow, *Salix laevigata* Bebb (Malpighiales: Salicaceae), every week for 4 to 5 mo. No polyphagous shot hole borer adults emerged from chipped or unchipped coast live oak logs, suggesting this species is not a preferred reproductive host. However, following chipping, a small number of polyphagous shot hole borer adults emerged from boxelder (up to 7 wk) and from California sycamore and red willow (both up to 9 wk). A significantly greater number of polyphagous shot hole borer adults emerged from unchipped logs of boxelder (up to 14 wk) and California sycamore and red willow (both up to 5 mo). Chipping of boxelder, California sycamore, and red willow by using common commercially available chippers reduced polyphagous shot hole borer emergence by over 97%. Emerged polyphagous shot hole borer adults were strongly female-biased, regardless of host. Chipping treatments were highly effective, but for the complete elimination of polyphagous shot hole borer from woody material, other sanitation measures such as solarization in conjunction with chipping are recommended. Environmental and ecological impact of polyphagous shot hole borer is reviewed and discussed.

Key words: *Acer* spp., *Euwallacea* nr. *fornicatus*, invasive ambrosia beetle, Kuroshio shot hole borer, tea shot hole borer

The invasive polyphagous shot hole borer, tea shot hole borer, and Kuroshio shot hole borer are three members in the cryptic species complex *Euwallacea* nr. *fornicatus* (Eichhoff) (Coleoptera: Curculionidae: Scolytinae) (Coleman et al. 2013, Stouthamer et al. 2017, Gomez et al. 2018, Smith et al. 2019). Smith et al. (2019) recently proposed new taxonomic classifications for the three cryptic species, but these new classifications conflict with previous studies (O'Donnell et al. 2015, Stouthamer et al. 2017). Polyphagous shot hole borer in Los Angeles, California, is morphologically similar to Kuroshio shot hole borer, which was discovered in San Diego, California, and tea shot hole borer (Eskalen et al. 2013, Chen et al. 2017, Smith et al. 2019), which has been introduced into Florida and Hawaii, United States and several other countries (Li et al. 2015, Carrillo et al. 2016, Kendra et al. 2017). Besides the differences in cytochrome oxidase c subunit 1 (COI) among the three members, polyphagous shot hole borer and tea shot hole borer qualitatively and quantitatively differ in cuticular hydrocarbon profile (Chen et al. 2017). Comparison of cuticular hydrocarbon profiles between polyphagous shot hole borer and Kuroshio shot hole borer, and between Kuroshio shot hole borer and tea shot hole borer have yet to be investigated.

Native to southeastern Asia, polyphagous shot hole borer has internationally spread to South Africa, Israel, and United States (Paap et al. 2018, Coleman et al. 2019). Since its initial detection in 2003 in Los Angeles County, California, United States (Eskalen et al. 2013, Seybold et al. 2015), polyphagous shot hole borer has spread or been secondarily introduced into five neighboring counties (Orange, Riverside, San Bernardino, San Diego, and Ventura) in southern California. The movement of the original population of polyphagous shot hole borer in southern California is likely the result of natural dispersal of females or *via* the movement of green waste material (T.W.C., personal observation). No inter-county quarantines are currently established in California to regulate the movement of potentially polyphagous shot hole borer-infested host material, which further complicates the management of this species. The exotic ambrosia beetle carries several symbotic fungi, but one fungal species, *Fusarium euwallaceae* (Hypocreales: Nectriaceae), has been linked to tree dieback, referred to as 'Fusarium dieback' (Eskalen et al. 2013, Eskalen et al. 2015, O'Donnell et al. 2015). The main cause of tree mortality is likely the disruption of water and nutrients in the phloem and xylem, which results from both fungal infection and extensive beetle boring (Coleman et al. 2019). High-levels of colonization by female polyphagous shot hole borer and the ensuing action of the pathogen along the main stem and branches have led frequently to tree injury and mortality of certain hardwood species (Coleman et al. 2019).

Polyphagous shot hole borer and it's closely related Kuroshio shot hole borer, and tea shot hole borer pose a great ecological and environmental threat to infested areas (Coleman et al. 2019, Boland et al. 2020) by attacking a wide range of ornamental, and agriculturally important hardwood species hosts and reproducing successfully in approximately 40 native tree species (Eskalen et al. 2013, Chen et al. 2014, O'Donnell et al. 2015, Carrillo et al. 2016). For instance, the loss of tree canopy cover in the riparian area due to Kuroshio shot hole borer in the Tijuana River Valley has led to growth and expansion of invasive weeds such as *Arundo donax* L. (Poales: Poaceae) (Boland et al. 2020). They are also potential pests to avocado, *Persea americana* Mill. (Laurales: Lauraceae), which is a major agricultural tree in California and Florida (Eskalen et al. 2013, Carrillo et al. 2016).

Tree injury and mortality of hardwood species from polyphagous shot hole borer have been observed most frequently in *Acer* spp., *Salix* spp., and *Platanus* spp. during ground surveys of urban and native stands in southern California (Coleman et al. 2013, Coleman et al. 2019). Branch and stem failure have also occurred on heavily colonized trees due to extensive mining of the xylem by adults of this wood-boring beetle. Polyphagous shot hole borer likely completes several generations a year (i.e., multi-voltinism) in the urban areas of southern California and the beetle flight has been recorded year-round (Y.C. et al., unpublished data). Multivoltine reproduction is also supported by a laboratory rearing study using a sawdust-based diet (Cooperband et al. 2016). The species is haplodiploid (i.e., males develop from unfertilized eggs and are haploid, whereas females develop from fertilized eggs and are diploid). Males are flightless, and females and males can be distinguished by body color, length, and presence/absence of the pair of membranous hind wings. It undergoes three larval instars (Chen et al. 2017).

An effective integrated pest management (IPM) program for an invasive wood-boring insect usually includes early detection and eradication; effective insecticide treatments; prevention of movement of infested wood from the zone of infestation; and chipping or grinding infested woody material on site. Quercivorol and α-copaene attract *Euwallacea* nr. *fornicatus* (Kendra et al. 2017). Preventing movement of infested wood from the infested areas and chipping infested wood are effective in slowing the spread of many invasive wood-boring insects (Haack et al. 2010; Jones et al. 2013, Spence et al. 2013). For example, grinding coast live oak, *Quercus agrifolia* Née (Fagales: Fagaceae), to a 7.6 cm or smaller particle size significantly reduced emergence of the invasive goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), in San Diego County, California (Jones et al. 2013). This management option is effective for large quantities of wood and more effective than other sanitation options such as debarking or solarization for goldspotted oak borer (Jones et al. 2013).

The efficacy of chipping of *Acer negundo* L. (Sapindales: Sapindaceae), one of the primary hosts from the California urban forest, to manage populations of polyphagous shot hole borer in southern California was evaluated (Jones and Paine 2015). These authors found that chipping to less than 5 cm reduced polyphagous shot hole borer 'activity' (i.e., 'number of boring dust mounds per kilogram chipped material') in trials in 2012 and 2014. They also found that this treatment significantly reduced polyphagous shot hole borer emergence (i.e., 'beetles per kilogram material') in the 2014 trial, and although statistically nonsignificant (due to overall low beetle emergence), the chipping numerically reduced polyphagous shot hole borer emergence in the 2012 trial. The effectiveness of chipping cut logs of other frequently planted southern California hardwood trees and potentially vulnerable polyphagous shot hole borer hosts, such as California sycamore, *Platanus racemosa* Nutt. (Proteales: Platanaceae), coast live oak, *Quercus agrifolia* Née, and red willow, *Salix laevigata* Bebb (Malpighiales: Salicaceae), in reducing polyphagous shot hole borer spread remains unknown. Dynamics of polyphagous shot hole borer female and male survival on chipped and unchipped cut logs, and the sex ratio has not been reported in the literature.

Therefore, we investigated the effectiveness of chipping cut logs of several key hosts, which are also abundant urban and native tree species, with the focus on collecting suitably infested material to maximize emergence from the control (untreated) logs. With this approach, we were also able to evaluate the emergence dynamics with an emphasis on the behavior of both male and female polyphagous shot hole borer and other subcortical insects in the community of organisms that accompany these dying hardwoods. The goal of our experiments was to reduce polyphagous shot hole borer emergence (and not an indirect measure of 'activity') and to investigate polyphagous shot hole borer reproduction within cut logs. We reasoned that results of research of this nature would also be important for establishing guidelines for time limits for holding cut wood before releasing it out of infested areas. Due to the taxonomic confusion surrounding several *Euwallacea* nr. *fornicatus* species, we used cuticular hydrocarbon profiles and location of plant/insect collection to verify the species in the study. As a result, we also developed support to infer the development of polyphagous shot hole borer within felled logs by monitoring polyphagous shot hole borer adult emergence periodically until no further adult emergence occurred.

Methods and Materials

2014 Chipping Experiment

Three host plant species (California sycamore, coast live oak, and red willow) were evaluated. One dying and polyphagous shot hole borer -infested California sycamore (diameter at breast height [DBH] of 45.47 cm) was felled on 18 January 2014 (Glendora, CA, N 34.245532°, W 117.834767°). Five polyphagous shot hole borer-infested red willow trees (mean DBH of 7.98 ± 1.24 cm) and one polyphagous shot hole borer-infested coast live oak tree (8.38 cm

DBH) were also felled on 18 January 2014 in Pasadena Glen (Pasadena, CA, N 34.182641°, W 118.078742°). The main stem and branches with polyphagous shot hole borer attacks were cut into approximately 38 cm sections. These sections were selected based on high-levels of wet, dark-colored staining; expelled boring dust; and adult polyphagous shot hole borer entry/emergence holes.

Chipping treatments were conducted on 18 January 2014 in Glendora, CA (N 34.245532°, W 117.834767°) with a 12-inch (30.5 cm) drum-style, hand-fed brush chipper (model # 990XP, Bandit Industries Inc., Remus, MI). Prior to chipping, logs from each tree species were randomly sorted into equal (in weight) chipped and unchipped control treatments. For the chipping treatment, all logs were chipped at the highest setting (i.e., largest wood chip size), which is used most frequently by local arborists. Each species was chipped individually and collected directly from the chipper in a 55 gallon (208 liters) plastic container. Unchipped logs and chips from each species were then transferred to five-gallon (19 liters) plastic containers. To ensure that replicates of each species were homogenous, wood chips and unchipped control log pieces were weighed (Taylor/Metro, China, Model # 2004D 1204 V2525) and separated equally into replicates. For example, California sycamore chips and control logs were 25.59 ± 1.95 and 27.51 ± 1.24 kg (n = 7 for both treatments), respectively, and the difference in weight was not significant ($F_{1,12}$ = 0.70, $P > 0.05$); coast live oak chips and control logs were 10.8 and 9 kg, respectively, and red willow chips and control logs were both 13.86 ± 4.41 kg (n = 5 for both treatments), and the difference in weight between chipped and unchipped red willow logs was not significant ($F_{1,8}$ = 0.00, $P > 0.05$). To gather a general idea of the chip size (length and width), the three longest and the 20 shortest pieces from each replicate were measured (Table 1).

After the individual replicates were established, chips and unchipped logs were monitored in five-gallon plastic containers covered with Trimaco elastic top paint strainer (Model # 11513, Trimaco, Morrisville, NC) or collapsible no-see-um tents (Model # 1466B, Bioquip, Rancho Dominguez, CA). Treatment replicates were monitored weekly for polyphagous shot hole borer adult (females and males counted separately) emergence until emergence ceased for 2 wk, which was approximately 5 mo. Polyphagous shot hole borer adults and other insects (Curculionidae, Nitidulidae, Sessiidae, Formicidae) were collected at least twice a day (a.m. and p.m.) with aspirators and stored in a freezer (0°C) until the insects could be identified and counted. Insects were collected from the surface of the chipped material or logs and from the plastic bucket rim and screening from the cages. Chipped wood was inspected daily for evidence of boring dust to assess for possible re-infestations. Wood was stored at constant room temperature. Polyphagous shot hole borer females and males were considered separately in the statistical analyses and presentation. Because no polyphagous shot hole borer were collected from both chipped and unchipped treatments of coast live oak, this host was excluded from further analysis.

2015 Chipping Experiment

Eight boxelder trees *A. negundo* infested with polyphagous shot hole borer were felled and chipped on 10 February 2015 from the Whittier Narrows Recreational Area, South El Monte, CA (N 34.032194°, W 118.070394°). From the main stem of each tree, two to four sections (~35 cm long) were collected. Replicates were established by partitioning the equal number of logs from the same tree into wood piles and one wood pile was selected randomly for the chipping treatment. The diameter of logs for chipped and unchipped control log treatments were 7.24 ± 0.58 and 7.21 ± 0.53 cm (n = 8 for both treatments), respectively. The difference in diameter between chipped and unchipped boxelder logs was insignificant ($F_{1,14}$ = 0.00, $P > 0.05$). The chipping treatments were conducted at the Dalton Fire Station, Angeles National Forest (in Glendora, CA, N 34.156038°, W 117.837530°) by using a Wood/Chuck Hyroller 1200 Controlled Feed Disc chipper (Shelby, NC) from the Dalton Fire Station, Los Angeles Ranger

Table 1. Lengths and widths of the longest and shortest chips (mean ± SE cm) in the experiments to assess the effect of chipping treatments on the emergence of the polyphagous shot hole borer in southern California

Year	Tree species	Log #	Longest pieces[a]		Shortest pieces[b]	
			Length	Width	Length	Width
2014	California sycamore	1	12.50 ± 2.65	5.48 ± 1.48	3.61 ± 0.28	2.07 ± 0.18
		2	7.30 ± 0.99	3.93 ± 0.09	2.39 ± 0.29	1.20 ± 0.06
		3	10.33 ± 2.14	4.30 ± 0.95	2.87 ± 0.23	1.52 ± 0.14
		4	9.37 ± 0.23	4.03 ± 0.41	2.34 ± 0.23	1.35 ± 0.14
		5	11.47 ± 1.57	7.57 ± 1.88	2.66 ± 0.32	1.38 ± 0.09
		6	9.40 ± 1.27	2.63 ± 0.72	3.37 ± 0.99	1.76 ± 0.31
		7	2.47 ± 1.45	3.30 ± 0.61	2.61 ± 0.22	1.79 ± 0.15
	Red willow	1	15.60 ± 2.97	2.10 ± 0.12	2.54 ± 0.24	1.49 ± 0.10
		2	14.10 ± 2.73	2.67 ± 0.87	3.22 ± 0.33	1.57 ± 0.10
		3	14.17 ± 1.09	2.70 ± 0.51	3.51 ± 0.65	1.46 ± 0.10
		4	11.10 ± 1.40	1.97 ± 0.12	3.00 ± 0.44	1.13 ± 0.10
		5	16.55 ± 3.74	3.77 ± 1.64	3.52 ± 0.38	1.70 ± 0.18
2015	Boxelder	1	65.67 ± 8.01	10.17 ± 3.63		
		2	49.73 ± 5.07	7.33 ± 1.04		
		3	54.13 ± 5.23	16.08 ± 1.34		
		4	44.80 ± 5.54	16.40 ± 1.47		
		5	46.33 ± 3.57	18.24 ± 1.13		
		6	51.61 ± 4.51	17.84 ± 0.88		
		7	28.81 ± 2.46	13.90 ± 0.78		
		8	43.50 ± 3.87	16.16 ± 0.95		

[a]The lengths and widths of three and 20 longest pieces from each log were measure in the studies in 2014 and the 2015, respectively.

[b]The lengths and widths of 20 shortest pieces from each log were measured in 2014 studies and the shortest pieces in 2015 were not measured.

District, Angeles National Forest. As mentioned previously, the wood was chipped at the highest setting (ie, to produce the largest chip size). Length and width of the 20 longest pieces from each log were measured (Table 1). Wood was enclosed and monitored as in the 2014 chipping study. Polyphagous shot hole borer females and males were considered separately in the statistical analyses and presentation.

Voucher specimens from both studies were deposited with the Department of Entomology, California Academy of Sciences, San Francisco, CA.

Verification of Polyphagous Shot Hole Borer

Identification of polyphagous shot hole borer was verified by morphological characteristics, location of plant/insect collection (Stouthamer et al. 2017; https://ucanr.edu/sites/pshb/pest-overview/ishb-fd-distribution-in-california/, last accessed 14 July 2020), and partially supported by cuticular hydrocarbon profiles detailed in Chen et al. (2017).

Statistical Analyses

All statistical analyses were conducted in SAS v. 9.4 (SAS Institute Inc., Cary, NC). A critical level of $\alpha = 0.05$ was used for all analyses. Cuticular hydrocarbon profiles of beetles collected from boxelder, California sycamore, and red willow were compared to those for polyphagous shot hole borer and tea shot hole borer detailed in Chen et al. (2017) with a test of association (χ^2; PROC FREQ in SAS). The Kolmogorov–Smirnov test and Levene's test were used to test normality and homogeneity of variance, respectively. Total polyphagous shot hole borer females collected in 2014 from chipped and unchipped red willow were normally distributed, and they were analyzed and compared by a one-way ANOVA (PROC GLM in SAS). Total polyphagous shot hole borer females and males collected in 2014 from chipped and unchipped California sycamore, total polyphagous shot hole borer males collected in 2014 from red willow, and total polyphagous shot hole borer females and males collected in 2015 from boxelder were not normally distributed, and they were analyzed by a non-parametric Kruskal–Wallis test (PROC NPAR1WAY in SAS). DBH and weight of chipped and unchipped logs in all studies were analyzed by a one-way ANOVA (see above).

Results

Verification of Polyphagous Shot Hole Borer

The two dominant cuticular hydrocarbons of beetles emerged from boxelder, California sycamore, and red willow were compound peak

Table 2. Cuticular hydrocarbons[a] extracted from polyphagous shot hole borer, *Euwallacea* nr. *fornicatus* collected from three host plants in the current study

Peak #	Compound[b,c]	Boxelder		California sycamore		Red willow	
		243 Females	49 Males	245 Females	29 Males	245 Females	136 Males
1	C27	0.21	0.00	0.37	0.00	0.65	1.38
2	11-meC27	0.00	0.00	0.00	0.00	0.00	0.00
3	14-meC28	0.00	0.00	0.00	0.00	0.00	0.00
4	C29	1.94	1.33	2.33	1.07	3.69	4.60
5	15-; 13-; 11-meC29	0.67	0.72	0.58	0.45	0.89	1.53
6	13,17-; 11,15-dimeC29	0.83	0.55	1.19	0.74	0.96	1.09
7	7,X-dimeC29 + 3-meC29	0.10	0.00	0.24	0.00	0.13	0.71
8	5,15-dimeC29	0.00	0.00	0.00	0.00	0.08	0.00
9	C30	0.39	0.00	0.50	0.43	0.57	0.71
10	15-; 14-; 13-; 12-meC30	0.19	0.00	0.16	0.00	0.26	0.39
11	13,17-; 12,16-dimeC30	0.73	0.49	1.01	0.75	1.37	0.90
12	C31	1.00	0.58	1.23	0.40	1.72	2.14
13	15-; 13-; 11-meC31	6.06	5.84	2.70	2.89	4.74	5.50
14	13,17-dimeC31; 7,19; 7,17-dimeC31	36.09	41.99	35.11	46.61	33.99	34.74
15	2-meC31; 5,15-; 5,17-; 5,19-dimeC31; 11,15,19-; 9,13,17-trimeC31	1.55	1.13	2.61	1.89	2.01	2.03
16	7,13,17-; 7,11,17-trimeC31	0.59	0.24	0.84	0.53	0.65	0.82
17	**5,X,X-trimeC31**	0.41	0.00	0.73	0.32	0.61	0.66
18	16-;15-;14-;13-;12-meC32	0.41	0.25	0.60	0.31	0.53	0.62
19	14,18-; 13,17-; 12,16-dimeC32	3.30	2.69	3.79	3.12	3.47	3.12
20	17-; 15-; 13-; 11-meC33	1.82	1.37	1.29	0.94	2.23	2.57
21	15,19-; 13,17; 11,21; **9,21**-dimeC33	36.71	38.39	35.71	34.67	32.50	29.55
22	5,15-; 5,17-; 5,19-; 5,21-dimeC33; 9,13-17-; 11,X,X-trimeC33	2.54	2.10	3.54	2.44	2.96	2.54
23	**5,X,X-trimeC33**	0.81	0.50	1.17	0.50	1.45	0.81
24	14,18-; 13,17-; 12,16-dimeC34	0.70	0.39	0.87	0.45	0.86	0.63
25	17-meC35	0.14	0.00	0.17	0.00	0.36	0.46
26	15,19-; 13,17-; 11,23-dimeC35	2.42	1.44	2.66	1.20	2.67	2.08
27	**11,17,23-trimeC33**	0.40	0.00	0.59	0.28	0.65	0.43

[a]Percentage of total hydrocarbon.

[b]This shorthand uses a descriptor for the total number of carbons (CXX) in the hydrocarbon component, excluding the methyl branch(es), and the location of methyl groups (X-me) (see text).

[c]Cuticular hydrocarbons listed in bold type indicate tentative identifications.

14 and 21, which is characteristic of polyphagous shot hole borer (Table 2 in the current study and Table 5 in Chen et al. 2017). The two dominant compounds of tea shot hole borer were peak # 5 and 6. Test of association showed that the cuticular hydrocarbon profiles of beetles in the current study did not differ from those of polyphagous shot hole borer, but differed from those of tea shot hole borer, both reported in Chen et al. (2017), regardless of host plant species. The cuticular hydrocarbon profiles of males and females did not differ from each other, regardless of host plant species. Besides morphological characteristics, the beetles monitored were identified as polyphagous shot hole borer, not tea shot hole borer.

2014 Chipping Experiment

A total of 36 polyphagous shot hole borer females and four polyphagous shot hole borer males emerged from chipped California sycamore logs between January 20 and June 19. Females accounted for 90.0% of all polyphagous shot hole borer emerged from chipped logs. A total of 14,539 polyphagous shot hole borer females and 936 polyphagous shot hole borer males emerged from unchipped California sycamore logs between January 20 and June 19. Females accounted for 94.0% of all polyphagous shot hole borer emerged from unchipped logs. Emergence of polyphagous shot hole borer females from chipped California sycamore logs ceased 3 mo after initiation of the experiment, whereas 563 polyphagous shot hole borer females emerged from unchipped California sycamore logs between 4 and 5 mo after the experiment was initiated. Emergence of polyphagous shot hole borer males from chipped California sycamore logs ceased 3 mo after initiation of the experiment, whereas 45 polyphagous shot hole borer males emerged from unchipped sycamore logs between 4 and 5 mo after the experiment was initiated. The number of polyphagous shot hole borer female and male emergence from chipped logs was consistently low and peaked (March 14; 10 females and three males) 54 d after the onset of the experiment, whereas emergence from the control logs was much higher and peaked (March 21; 2,183 females and 93 males) around 60 d following the first beetle collection for both females and males (Fig. 1). Chipping significantly reduced the number of female ($\chi^2_1 = 9.80$, $P < 0.01$; Fig. 2A) and male ($\chi^2_1 = 10.62$, $P < 0.01$; Fig. 2B) polyphagous shot hole borer collected. The mean number of polyphagous shot hole borer females collected from chipped and unchipped logs was 5.71 ± 1.90 and 2,077.00 ± 246.51 per log, respectively (Fig. 2A); the mean number of polyphagous shot hole borer males collected from chipped and unchipped logs was 0.14 ± 0.14 and 133.71 ± 16.01 per log, respectively (Fig. 2B).

A total of 15 polyphagous shot hole borer females and zero polyphagous shot hole borer males emerged from chipped red willow logs between January 20 and June 19. Females accounted for 100.00% of all polyphagous shot hole borer emerged from chipped logs. A total of 535 polyphagous shot hole borer females and 48 polyphagous shot hole borer males emerged from unchipped red willow

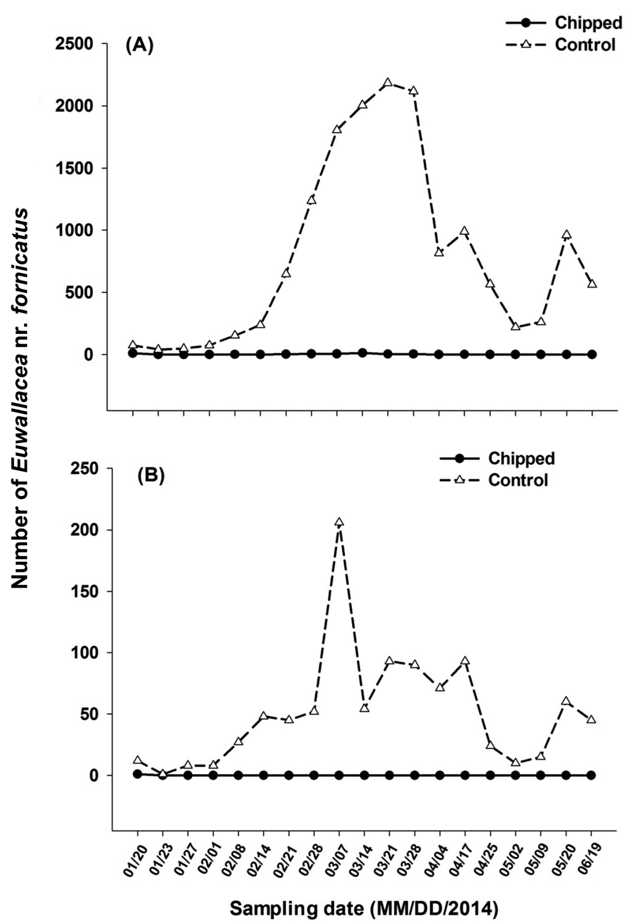

Fig. 1. Emergence of polyphagous shot hole borer, *Euwallacea* nr. *fornicatus*, over time from January to June 2014 from chipped and unchipped California sycamore, *Platanus racemosa*. (A) Females; (B) Male.

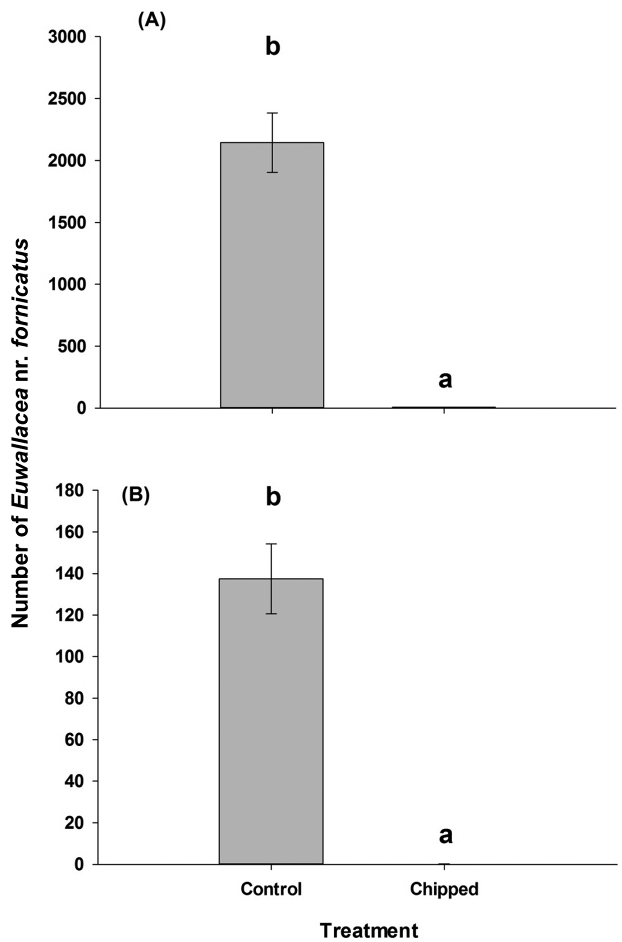

Fig. 2. Mean total (±1 SE) emergence of polyphagous shot hole borer, *Euwallacea* nr. *fornicatus*, in 2014 from chipped and unchipped California sycamore, *Platanus racemosa*. (A) Females; (B) Male ($n = 7$).

logs between January 20 and June 19. Females accounted for 91.8% of all polyphagous shot hole borer emerged from unchipped logs. No polyphagous shot hole borer females emerged from chipped red willow logs after 3 mo had elapsed from when the experiment was initiated, whereas 53 polyphagous shot hole borer females emerged from unchipped red willow logs between 4 and 5 mo after the experiment was initiated. No polyphagous shot hole borer males emerged from chipped red willow logs after 3 mo had elapsed from when the experiment was initiated, whereas six polyphagous shot hole borer females emerged from unchipped red willow logs between 4 and 5 mo after the experiment was initiated. The number of polyphagous shot hole borer females and males collected from chipped red willow logs was consistently low and peaked (April 17; 14 females and zero male) 85 d after initiation of the experiment, whereas that from control unchipped logs was much higher and peaked (April 17; 143 females and 42 males) 85 d following the first beetle collection (Fig. 3). Chipping significantly reduced the number of polyphagous shot hole borer females ($F_{1,8}$ = 10.19, P < 0.05) and males ($\chi_1^2 = 5.58$, P < 0.05) collected. The mean numbers of polyphagous shot hole borer females collected from chipped and unchipped logs of red willow were 3.00 ± 1.48 and 106.80 ± 32.49 per log, respectively (Fig. 4A); the mean numbers of polyphagous shot hole borer males collected from chipped and unchipped logs of red willow were 0.00 ± 0.00 and 9.60 ± 8.13 per log, respectively (Fig. 4B).

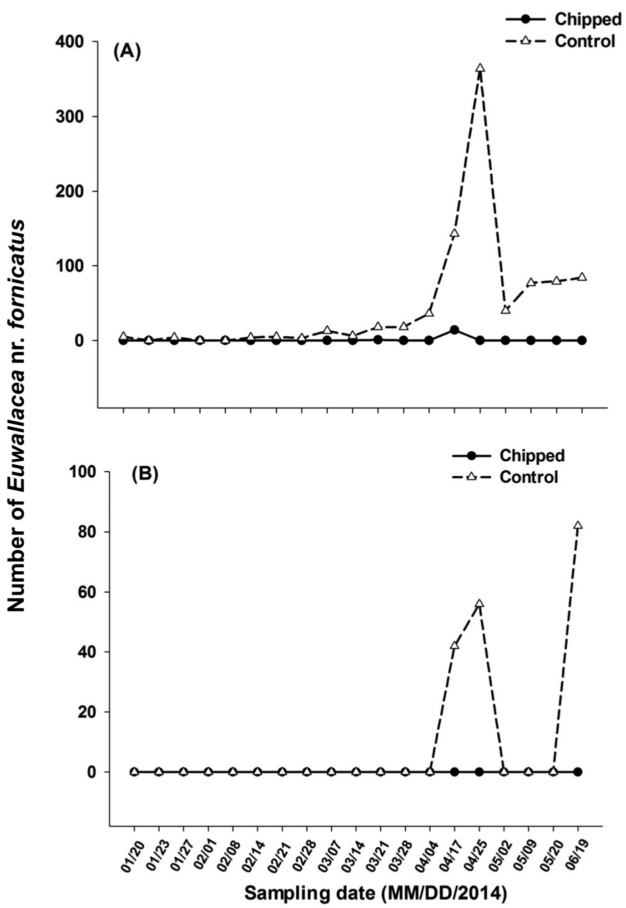

Fig. 3. Emergence of polyphagous shot hole borer, *Euwallacea* nr. *fornicatus*, over time from January to June 2014 from chipped and unchipped red willow, *Salix laevigata*. (A) Females; (B) Male.

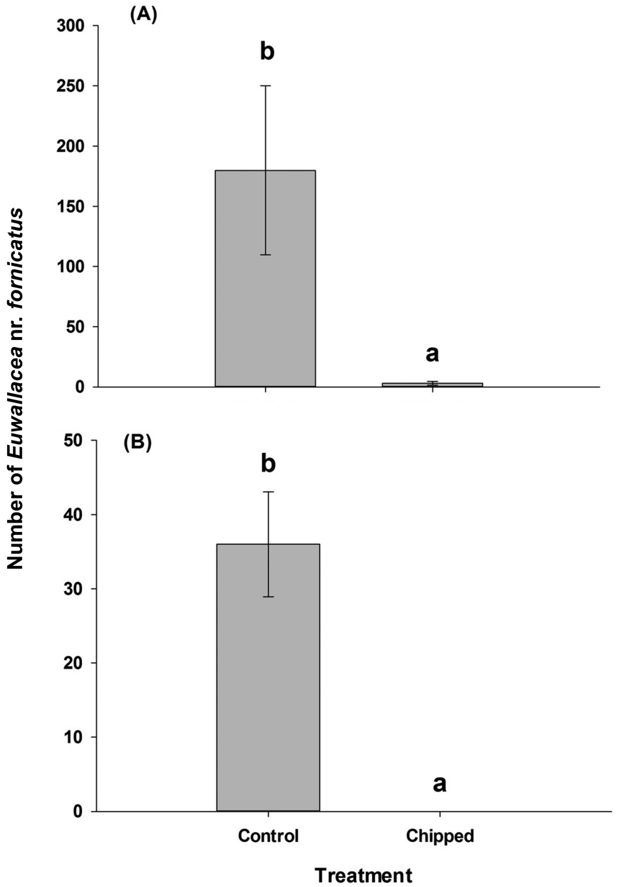

Fig. 4. Mean total (±1 SE) emergence of polyphagous shot hole borer, *Euwallacea* nr. *fornicatus*, in 2014 from chipped and unchipped red willow, *Salix laevigata*. (A) Females; (B) Male (n = 5).

2015 Chipping Experiment

A total of 7 polyphagous shot hole borer females and zero polyphagous shot hole borer males emerged from chipped boxelder logs between February 12 and June 11. Females accounted for 100.0% of all polyphagous shot hole borer emerged from chipped logs. A total of 1,043 polyphagous shot hole borer females and 174 polyphagous shot hole borer males emerged from unchipped boxelder logs between February 12 and June 11. Females accounted for 85.7% of all polyphagous shot hole borer emerged from unchipped logs. Emergence of polyphagous shot hole borer females from chipped boxelder logs ceased 50 d after the initiation of the experiment, whereas one polyphagous shot hole borer female emerged from unchipped boxelder logs nearly 4 mo after the experiment was initiated. No polyphagous shot hole borer males emerged from chipped boxelder logs throughout the experiment, whereas two polyphagous shot hole borer males emerged from unchipped boxelder logs 3 mo after the experiment was initiated. The number of polyphagous shot hole borer females and males collected from chipped boxelder logs was consistently low and peaked (February 12; 3 females and zero male) at the first collection, whereas that from control unchipped logs was much higher and peaked (April 23; 243 females and 49 males) 71 d following the first beetle collection (Fig. 5). Chipping significantly reduced the number of polyphagous shot hole borer females ($\chi_1^2 = 11.43$, P < 0.001) and males ($\chi_1^2 = 12.89$, P < 0.001) collected. The mean numbers of polyphagous shot hole borer females collected from

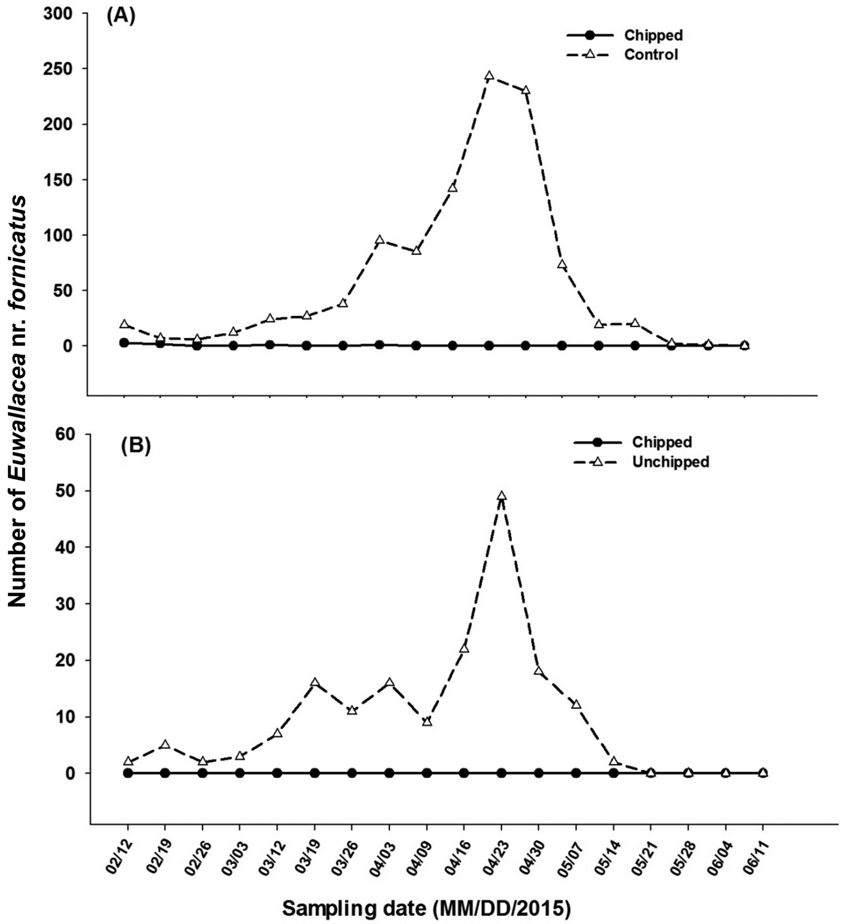

Fig. 5. Emergence of polyphagous shot hole borer, *Euwallacea* nr. *fornicatus*, over time from February to June 2015 from chipped and unchipped boxelder, *Acer negundo*. (A) Females; (B) Male.

chipped and unchipped logs of boxelder were 1.00 ± 0.38 and 129.75 ± 46.29 per log, respectively (Fig. 6A); the mean numbers of polyphagous shot hole borer males collected from chipped and unchipped logs of red willow were 0.00 ± 0.00 and 19.88 ± 6.39 per log, respectively (Fig. 6B).

In 2014, a total of 134 other insects emerged, including nitidulids (24), other ambrosia beetles (25), ants (82), and three clearwing moth (Sessiidae) from chipped and unchipped logs. In 2015, a total of 30 other insects emerged, including Diptera (17), Hymenoptera (12), and Coleoptera (Monotomidae, *Rhizophagus* sp.) (1) from chipped and unchipped logs. The adult Diptera in the samples were often accompanied by pupal exuviae (18) that indicated that the unidentified Hymenoptera may have been parasitoids of the flies.

Discussion

Environmental, ecological, and economic costs associated with invasive species are well documented (Pimentel et al. 2005, Brockerhoff et al. 2006, Keins et al. 2009). Polyphagous shot hole borer causes tree death in many native tree species (Eskalen et al. 2013, Chen et al. 2014, Coleman et al. 2019). To mitigate impacts of polyphagous shot hole borer, early detection, and effective elimination is critical. Felling and chipping are important measures in slowing the spread of many invasive insects (McCullough et al. 2007, Jones et al. 2013, Jones and Paine 2015).

In this study, chipping of California sycamore, red willow, and boxelder significantly reduced polyphagous shot hole borer survival. Assuming similar numbers of potential polyphagous shot hole borer adults in chipped and unchipped logs before treatment, chipping of California sycamore, red willow, and boxelder, reduced polyphagous shot hole borer adult emergence by 99.8, 97.21, and 99.3%, respectively. Chip size relative to beetle size determines the effectiveness of chipping as a sanitation method. Chipping of coast live oak logs to <7.5 cm completely killed goldspotted oak borer adults in the logs (Jones et al. 2013). Chipping of green ash, *Fraxinus pennsylvanica* Marsh. (Lamiales: Oleaceae), logs to 5 cm, however, could not completely eliminate prepupae of the invasive emerald ash borer (McCullough et al. 2007). Sizes of goldspotted oak borer and emerald ash borer adults are similar, and both are much larger than that of polyphagous shot hole borer. Chipping of boxelder logs to <5 cm could not entirely eliminate activity of polyphagous shot hole borer adults (Jones and Paine 2015). Therefore, although chipping is effective in reducing polyphagous shot hole borer emergence in infested logs, for a complete elimination, the chip size needs to be smaller or other measures may be needed, such as solarization (Jones and Paine 2015) in conjunction with chipping. Since polyphagous shot hole borer feeds in the xylem of host trees, debarking, as an effective measure for reducing emerald ash borer and goldspotted oak borer, would likely be ineffective in reducing the population density of polyphagous shot hole borer.

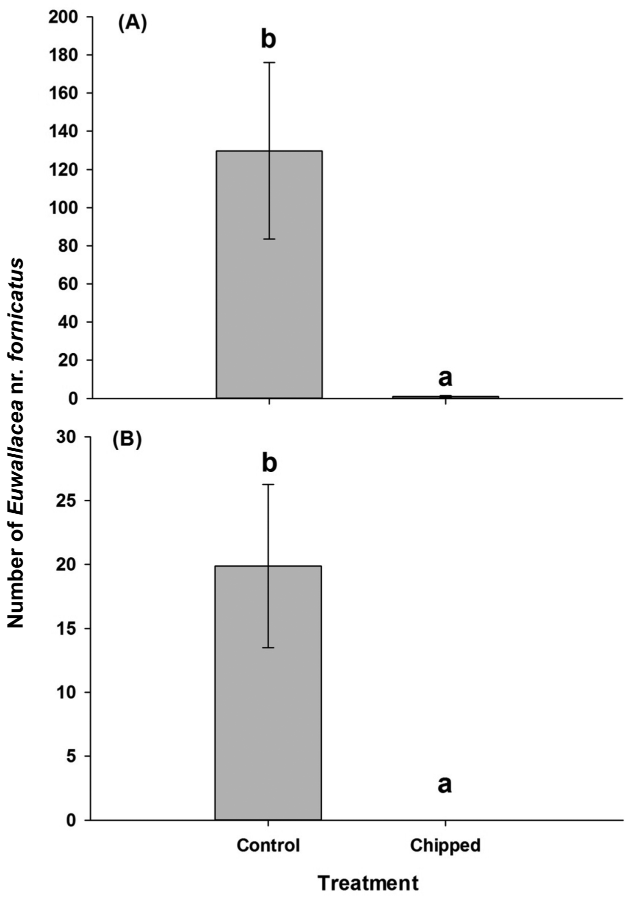

Fig. 6. Mean total (±1 SE) emergence of polyphagous shot hole borer, *Euwallacea* nr. *fornicatus*, in 2015 from boxelder, *Acer negundo*. (A) Females; (B) Male (n = 8).

The duration that an invasive pest survives in wood, either chipped or unchipped, is a critical consideration when implementing chipping as a management option. We found that a small number of polyphagous shot hole borer adults continued to emerge from chipped boxelder for 7 wk, and from chipped California sycamore and red willow for 9 wk following the chipping. Jones and Paine (2015) also observed polyphagous shot hole borer activity for 10 wk following the chipping of boxelder logs, which likely reflects activity by newly emerged adults. On the contrary, in our study, a large number of polyphagous shot hole borer adults continued to emerge from unchipped boxelder logs for three and a half months and from California sycamore and red willow logs for 5 mo following the felling of the host trees and the initiation of the study. Jones and Paine (2015), however, were uncertain whether the emergence activity in their study was caused by new polyphagous shot hole borer adults that developed from eggs, larvae, or prepupae that survived the chipping process, or was caused by polyphagous shot hole borer adults that survived the chipping process. They had observed the survival of some polyphagous shot hole borer adults in the absence of food for 8 wk. Little is known about the life history of polyphagous shot hole borer. By dissecting a large number of infested host logs and examining head capsule widths, Chen et al. (2017) determined that polyphagous shot hole borer has three larval instars. The exact developmental times of egg, each larval instar, prepupae, adult of polyphagous shot hole borer has not been studied, although times from initiation of a colony (i.e., by placing a single mated foundress in test tubes with a diet) to various stages were observed in laboratory setting (Cooperband et al., 2016). For instance, a whole generation of polyphagous shot hole borer takes approximately 22~24 d under 16:8 (L:D) h at 24°C. Gadd (1941) and Kumar et al. (2011) reported a developmental time of about 40 d from egg to adult death of tea shot hole borer. The environmental variables such as temperature and humidity in these reports are unclear. Assuming similar life history of polyphagous shot hole borer to tea shot hole borer and given the large number of beetles, we speculated that these polyphagous shot hole borer adults likely developed from eggs laid after the start of the experiment, and at least one generation of polyphagous shot hole borer develops within the logs in current study. This corroborates with the observation that polyphagous shot hole borer likely completes several generations a year in the urban areas of southern California and the beetle flight has been recorded year-round (Chen et al., unpublished data). For unchipped California sycamore and red willow logs, the large number of polyphagous shot hole borer adults emerging 5 mo following the setup of experiments indicates more generations may continue to develop. Therefore, to avoid the spread of polyphagous shot hole borer to new areas, unchipped hardwoods infested with polyphagous shot hole borer should not be moved out of the infested area at least 5 mo following the fell of the tree. The big difference in the number of polyphagous shot hole borer adults emerging from California sycamore and red willow manifests the need for differential handling of different host trees of size and susceptibility. Further studies are needed to elucidate the maximum survival times of polyphagous shot hole borer and in these host trees and the differences among various host trees.

The differences in polyphagous shot hole borer emergence observed with different tree species might indicate their suitability as reproductive hosts. No polyphagous shot hole borer adults emerged from coast live oak, although the log selected for this study contained many entrance holes. This suggests that coast live oak is a poor substrate for polyphagous shot hole borer fungal symbionts on which the beetle relies for nutrition, and subsequently reproduction, which is corroborated by many field observations that polyphagous shot hole borer attacks coast live oak but frequently does not result in progeny (Coleman et al. 2019). Therefore, sanitation of polyphagous shot hole borer on coast live oak may be unnecessary.

In summary, results of this study indicate that 1) chipping significantly reduces polyphagous shot hole borer emergence (>97%); 2) polyphagous shot hole borer adults can survive and/or reproduce in infested hardwood trees chipped by a commercial chipper for up to 3 mo; 3) polyphagous shot hole borer adults can survive and/or reproduce in felled and unchipped logs for over 5 mo; 4) Survival/reproduction of polyphagous shot hole borer differs by host species, and therefore the necessity and length of sanitation may also differ by species; and 5) polyphagous shot hole borer population is strongly female-dominated, regardless of host tree or chipping treatment. The results found for polyphagous shot hole borer in this study may also apply to the other members from the same cryptic species complex, since they are all very similar in ecology, life history, nutritional requirements, etc.

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Dedication

We dedicate this article to S.J.S. for his life-long contributions to the chemical ecology and management of forest pests. Tragically, Steve passed away in the middle of the submission of this work.

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