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Multiple-Lure Surveillance Trapping for *Ips* Bark Beetles, *Monochamus* Longhorn Beetles, and *Halyomorpha halys* (Hemiptera: Pentatomidae)

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Abstract

Invasions by insects introduced via international trade continue to cause worldwide impacts. Surveillance programs using traps baited with host volatiles and pheromones can detect incursions of nonnative species. We report on two experiments executed to determine if attractants for several insect species can be combined without compromising trap catches and detection ability of target species. In the first experiment, we tested the effect of bark beetle pheromones (plus α-pinene) and trap contact with foliage on trap catches of the brown marmorated stink bug *Halyomorpha halys* Stål (Hemiptera: Pentatomidae) in traps baited with a mixture of bisabolenes and methyl (*E,E,Z*)-2,4,6-decatrienoate. Trap capture of *H. halys* adults was greater in traps not in contact with foliage, and the bark beetle pheromones ipsenol and ipsdienol did not affect trap capture of *H. halys*. In the second experiment, we tested the effects of multi-lure interactions among the primary host attractants α-pinene and ethanol, and the pheromones monochamol, ipsenol, ipsdienol, lanierone, and the *H. halys* compounds, on trap captures of various forest and agricultural insect pests. Specifically, we targeted *Monochamus* spp. (Coleoptera: Cerambycidae), *Ips* spp. (Coleoptera: Scolytinae) and *H. halys*. We found that a combination of all lures did not catch significantly lower numbers of *Monochamus carolinensis* Olivier, *Monochamus scutellatus* Say (Coleoptera: Cerambycidae), and *Ips pini* Say (Coleoptera: Scolytidae) than lure combinations missing components although removal of both lanierone and ipsdienol somewhat increased catches of *Ips grandicollis* Eichhoff (Coleoptera: Curculionidae). Our results support the use of traps baited with a full combination of these attractants in surveillance programs. This should reduce costs and increase detection rates of a wider range of conifer forest pests and *H. halys*.

Key words: biological invasions, host volatiles, multiple-lure trapping, pheromones, surveillance

Globalization and the accompanying increased volume of goods traded internationally have resulted in many invasions of nonnative species into novel environments (Levine and D'Antonio 2003, Hulme 2009, Brockerhoff and Liebhold 2017). Insects threatening forests and agriculture are arriving via numerous pathways (Aukema et al. 2010, Brockerhoff et al. 2014, Liebhold et al. 2016a). International phytosanitary policies, such as the International Standards for Phytosanitary Measures (ISPM), have been implemented to reduce the number of insect species arriving at ports-of-entry via solid wood packaging material (ISPM 15) and live plants (ISPM 36), two dominant pathways responsible for alien forest insect and disease invasions (Liebhold et al. 2012, Haack et al. 2014). However, it is unlikely that these policies will prevent all insect species from arriving and establishing in new regions. Therefore, surveillance activities to detect recently arrived pests are an important line of defense for government agencies. Strategies aimed at preventing wider population establishment and spread are more likely to be successful if a species is detected early while its spread is limited and the populations are small (Bogich et al. 2008, Brockerhoff et al. 2010, Rassati et al. 2015, Liebhold et al. 2016b).

Early detection of nonnative insects can be time and labor intensive, and expensive (Blackburn et al. 2016). However, the cost of not having a surveillance program outweighs the alternative (Epanchin-Niell et al. 2014), and a diversified surveillance approach is optimal for detection (Yemshanov et al. 2014). Insect traps baited with synthetic primary host plant attractants (e.g., kairomones) and secondary attractants (e.g., pheromones) are widely used in surveillance and detection programs (Schwalbe and Mastro 1988, Brockerhoff et al. 2006). These typically target single species or species groups such as bark and ambrosia beetles. A growing body of evidence suggests that certain lure combinations can be used on the same trap for surveillance of multiple species, reducing costs of labor and materials without decreasing detection efficiency of individual target species due to interspecific disruption of responses (Witzgall et al. 2010, Wong et al. 2012, Brockerhoff et al. 2013, Rassati et al. 2014). While the multiple-lure technique has been investigated for species with similar life traits, very few studies have investigated the effects of attractants from different insect orders with differing life traits.

Monochamus spp. longhorned beetles (Coleoptera: Cerambycidae), *Ips* spp. bark beetles (Coleoptera: Curculionidae), and the brown marmorated stink bug (*Halyomorpha halys* Stål (Hemiptera: Pentatomidae)) are frequently intercepted at ports-of-entry. *Monochamus* spp. are feared because some species vector the pine wood nematode *Bursaphelenchus xylophilus* (Steiner and Buhrer) Nickle, which causes substantial mortality of pines in northeast Asia and Western Europe (Dwinell 1997, Mamiya 1988, Sousa et al. 2001). Most *Ips* spp. are secondary pests that attack stressed, dead or dying trees, but some species can reach epidemic proportions in their native and invaded range when conditions are suitable (e.g., *Ips typographus* L. [Europe] and *Ips pini* Say (Coleoptera: Scolytidae) [North America]). For example, the five-spined engraver *Ips grandicollis* Eichhoff (Coleoptera: Curculionidae) was introduced to Australia where it causes extensive tree mortality in pine plantations (Morgan 1989). *Halyomorpha halys*, native to Asia, invaded the United States and became a major agricultural pest of multiple economically important crops in a brief period of time (Leskey et al. 2012, Bergmann et al. 2016); *H. halys* is also established in mainland Europe and has been intercepted many times in Australia (Commonwealth of Australia 2015) and New Zealand (MacLellan 2013). Many countries carry out surveillance for these pests because they have the potential for causing significant ecological and economic losses.

Here our aim was to determine if attractants could be combined for the surveillance of multiple species across taxa belonging to different families and orders without significantly reducing catches of one or more target species. We evaluated *Ips* spp., *Monochamus* spp., and *H. halys* pheromone lures (along with the monoterpene α-pinene and ethanol) for effects on trap captures of these insects in two different experiments. Specifically, we tested the hypothesis that there would be no significant difference in catches of the target species by combining the attractants.

Materials and Methods

Experiment 1—Response of *H. halys* to Foliage and Bark Beetle Lures

We designed this experiment to test if bark beetle attractants interfered with captures of *H. halys*, and if trap captures of *H. halys* nymphs and adults increased when traps were in contact with foliage. The standard *H. halys* survey trap is a black pyramid trap with a 'DEAD-INN' jar and funnel (AgBio, Westminster, CO) attached to the top. We used a modified intercept panel trap (Alpha Scents, West Linn, OR), typically used to capture bark and wood-boring insects, with a 'DEAD-INN' jar and funnel attached to the top of the panel trap (Fig. 1) to collect *H. halys*. The collection jar at the top of the trap contained a 5-cm insecticidal (dichlorvos) kill strip (Hercon Vaportape II, Aberdeen Road Co., Emigsville, PA) which was replaced monthly. The collecting cup at the bottom of the trap contained soapy water (1 ml of unscented dish soap [Ultra Pure Clear, Colgate-Palmolive Co., New York, NY] per liter of water) as a drowning solution and was replaced weekly when the traps were serviced. Traps were spaced ~14 m apart. This experiment took place within a 1.5 ha abandoned hazelnut (*Corylus avellana* L.) orchard in Tualatin, Oregon (45°23′ N, 122°47′W) during October and November 2013. The perimeter of the orchard consisted of deciduous and coniferous trees. We installed all traps on hazelnut trees so that they were either in contact with tree foliage or at the end of the limb where traps hung in open space not in contact with tree foliage.

Compounds to attract the brown marmorated stink bug (*H. halys*) (combination #20 from a USDA patent application (Khrimian et al. 2014a), comprising a mix of 21% *cis*-epoxybisabolenols, 41% *trans*-epoxybisabolenols, and 37% 1,2,10,11-diepoxybisabolan-3-ol dispensed from a green plastic sachet, USDA, Kearneysville, WV) (Khrimian et al. 2014b) were combined with a separate grey septum containing methyl (*E,E,Z*)-2,4,6-decatrienoate (MDT, Alpha Scents, West Linn, OR). MDT is known as the pheromone of *Plautia stali* Scott (Hemiptera: Pentatomidae) and has been confirmed to act as a synergist, enhancing the attraction of *H. halys* (Weber et al. 2014).

Fig. 1. Modified panel trap (Alpha Scents, Inc. West Linn, OR) with a 'DEAD-INN' collection jar and funnel (sourced from AgBio, Westminster, CO) attached to the top of the panel trap (Photo credit: Peter Shearer Washington State University).

For the remainder of this manuscript, we refer to the combination of these two lures as the brown marmorated stink bug attractant or 'MSB'. To determine if attractants for key bark beetle and longhorn beetle species affected *H. halys* trap capture, some traps were baited with both the MSB attractants plus a three component bark beetle lure consisting of α-pinene (99.6%), racemic ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol; 0.2%), and racemic ipsenol (2-methyl-6-methylene-7-octen-4-ol; 0.2%) (Alpha Scents, West Linn, OR). Bark beetle attractants were released from either polyethylene bottles or bubblecaps and were placed in the middle of the panel trap. The MDT lures were replaced after 4 wk, and the #20 lures were replaced every 2 wk. The bark beetle lures were not replaced during this experiment. The *H. halys* attractant was placed in the 'DEAD-INN' jar. We checked traps weekly for 8 wk. Traps with either lure combination were deployed either inside the tree canopy directly touching foliage and limbs or suspended outside the canopy (not directly in contact with any plant parts) from a 6-mm-diameter nylon cord fastened to a tree limb. The tops of the suspended traps were approximately 2.4 m above ground level. The rationale for how traps were deployed pertains to recommendations for using panel traps for monitoring beetles (traps should be placed in line-of-sight from potential sources of beetles and not obscured by vegetation; USDA-APHIS 2011) or for deploying *H. halys* traps in trees (arboreal traps should touch plant parts to facilitate *H. halys* movement into traps) (Khrimian et al. 2008). There were 10 replicates of the four treatment combinations (foliage and lure treatments), with one randomly assigned combination per tree, and transects of four trees forming one replicate in a randomized complete block design.

Experiment 2—Responses of Cerambycidae, Curculionidae: Scolytinae, to Lure Combinations That Included the *H. halys* Lure

We evaluated the attraction of target insects to traps baited with various combinations of components (Table 1). α-Pinene and ethanol ('AE') are host-produced primary attractants that are broadly attractive to many bark and wood boring beetles, especially those attacking Pinaceae (Miller 2006, Miller and Rabaglia 2009). They enhance captures of many bark and wood-boring beetles to traps baited with pheromones (Hanks et al. 2012; Miller et al. 2013a, 2015a,b). Monochamol ('M'; 2-undecyloxy-1-ethanol), identified as a pheromone for *Monochamus galloprovincialis* Olivier (Pajares et al. 2010), *M. alternatus* Hope (Teale et al. 2011), *Monochamus scutellatus* Say (Coleoptera: Cerambycidae) (Fierke et al. 2012), *Monochamus carolinensis* Olivier (Allison et al. 2012), *Monochamus titillator* Fabricius (Allison et al. 2012), and *Monochamus sutor* L. (Pajares et al. 2013), has been used to trap *Monochamus* spp. longhorned beetles (Macias-Samano et al. 2012, Miller et al. 2016, Skabeikis et al. 2016). Ipsenol ('I') attracts *I. grandicollis* (Allison et al. 2012) whereas racemic ipsdienol attracts *I. pini* (Lanier et al 1972, Teale and Lanier 1991, Seybold et al. 1992, Miller et al. 1997). Lanierone (2-hydroxy-4,4,6-trimethyl-2,5-cyclohexadien-1-one) synergizes attraction of *I. pini* to traps baited with ipsdienol (Teale et al. 1991; Miller et al. 1997, 2003) and appears to mitigate repellent effects from ipsenol on *I. pini* (Miller et al. 2005). In this study, lanierone and ipsdienol devices were always deployed in combination ('LI'). Using morphological characteristics, we were able to distinguish the sex for all *M. scutellatus* (Yanega 1996) and *I. pini* (Wood 1982) captured in the study.

We considered traps with only the MSB lure as controls for contrasts with beetle-targeting lures because no interactions between target beetle species and *H. halys* are known. All lures for this experiment were obtained from Synergy Semiochemicals Corp. (Burnaby BC, Canada), except for the MSB lure components, which were from AlphaScents (Portland, OR).

This experiment was conducted across six sites in Greene County, PA, during 4 wk between May and June 2014 (Table 2). All target insects were native to this region except for *H. halys*, which is native to northeast Asia. Traps were placed in stands of planted white pine, *Pinus strobus* L., mixed with deciduous trees or adjacent to deciduous forest and open farmland. At all sites, broadleaved trees were present less than 100 m from any of the traps. The selection of sites with both pines and broadleaved trees was done to ensure the presence of host trees and habitat for both pine-feeding beetles and presumably *H. halys*, respectively. Because the physical structure of the trap can also affect trap capture rates (Dodds et al. 2010, 2015), we used two types of traps for insect sampling: 1) a modified intercept panel trap (Fig. 1); and 2) a standard 12-unit funnel trap (Synergy Semiochemicals Corp). A kill strip (Hercon Vaportape II Insecticidal Strips, Great Lakes IPM. Vestaburg, MI) was placed in the top jar of the modified panel trap to prevent insect escape, and the bottom wet cup of both traps was filled with diluted propylene glycol (Prestone Low Tox Antifreeze, Prestone Products Corp., Danbury, CT) to reduce insect escape and predation.

Table 1. Lure combinations assessed for the effects on catches of *Monochamus* spp. *Ips* spp. and *Halyomorpha halys* in Greene County, Pennsylvania (experiment 2)

		Blends tested									
Lures	Abbreviation	1	2	3	4	5	6	7	8	9	Release rate
α-pinene & ethanol	AE	✓	✓	✓	✓	✓	✓		✓	✓	150 mg per day @ 20°C/10 mg per day @ 20°C
Ipsenol	I		✓		✓		✓		✓	✓	1.4 mg per day @ 25°C
Lanierone & ipsdienol	LI			✓	✓		✓		✓	✓	~ 0.02 mg per day @ 20°C/0.7 mg per day @ 25°C
Monochamol	M					✓	✓		✓	✓	0.75 mg per day @ 20°C
Multi-component *H. halys* lure[a]	MSB							✓	✓	✓	unknown
Panel trap	P	✓	✓	✓	✓	✓	✓	✓	✓		
Funnel trap	F									✓	

All lures were placed on panel traps except for the funnel trap with the full lure combination.

[a] Comprised a mix of 21% cis-epoxybisabolenols, 41% trans- epoxybisabolenols and 37% 1,2,10,11-diepoxybisabolan-3-ol represented by 16 stereoisomers (USDA patent appl., combination #20) with methyl (E,E,Z)-2,4,6-decatrienoate (MDT).

Table 2. Six study sites used for experiment 2

Site	Coordinates	Elevation
A	39°43′25″N, 80°3′35″W	320 m
B	39°46′50″N, 80°8′54″W	340 m
C	39°45′26″N, 80°7′46″W	330 m
D	39°49′13″N, 80°3′2″W	310 m
E	39°49′7″N, 80°2′51″W	325 m
F	39°49′9″N, 80°5′29″W	335 m

There were a total of nine lure/trap type combinations used in the study (Table 1). All traps were separated by a distance of ≥20 m and hung (with rope) on twine strung between two trees at a height of approximately 1.5 m. Traps were placed as far away from the base of the tree and ground vegetation as possible. Traps were checked every 6–8 d, with every trap checked a total of four times each, and all insects removed at each check. The trial was laid out as a Latinized resolvable block design with one complete replicate in a linear transect at each site, and three blocks of three traps per transect (John and Williams 1995). The designs were constructed with CycDesign (CycSoftware 2009), and was chosen to ensure even distribution of treatments along the transects across sites.

Statistical Analysis

All analyses were carried out using GenStat (GenStat Committee 2014). For *H. halys* in experiment 1 and each species of interest in experiment 2, we summed trap catches across all collections. These were analyzed with a hierarchical generalized linear modeling approach (HGLM, Lee et al. 2006) which extends the standard generalized linear model (McCullagh and Nelder 1989) to allow inclusion of random effects, in addition to fixed effects. The counts were analyzed with a Poisson distribution for the fixed effects (treatments, and contrasts between particular treatments), and a gamma distribution for random effects (replicates for experiment 1; sites, position within sites for experiment 2). Both fixed and random effects were fitted with a logarithmic link. Thus, assessment of treatment effects is an assessment of multiplicative changes in catch between treatments.

The importance of random effects was assessed by a chi-square test of the change in deviance on dropping the term, as implemented in GenStat's HGRTEST procedure (VSN International Ltd 2015). Only significant random effects were retained in the final analyses. Fixed effects, including specific contrasts between the treatments, were assessed similarly to random effects, using GenStat's HGFTEST procedure. Because the chi-square test in mixed models can be too liberal (Kenward and Roger 1997), the calculated chi-square statistic was assessed as an *F*-statistic, using the residual degrees of freedom as the denominator degrees of freedom. Results are presented as mean catch/trap with associated 95% confidence limits, which were obtained on the link (logarithmic) scale and back-transformed for presentation. Note that the upper confidence limit for a mean of 0 cannot be easily obtained, so is not provided.

Results

Experiment 1—*H. halys* Response to Foliage and Bark Beetle Lures

We captured 181 immature *H. halys* and 623 adult *H. halys* in this experiment. More than twice as many *H. halys* adults were captured in traps suspended in open space ($n = 428$) than in traps in contact with tree foliage ($n = 195$) ($F_{1,27} = 13.24$, $P = 0.001$), but no difference was observed for *H. halys* nymphs ($F_{1,27} = 0.02$, $P = 0.885$) (Fig. 2). The addition of α-pinene, ipsenol, and ipsdienol did not interfere with trap captures of *H. halys* adults ($F_{1,27} = 0.06$, $P = 0.810$ for the main effect and $F_{1,27} = 0.54$, $P = 0.451$ for the interaction with position) or nymphs ($F_{1,27} = 1.27$, $P = 0.253$ for the main effect and $F_{1,27} = 3.20$, $P = 0.085$ for the interaction with trap position) (Fig. 2). No bark beetles were captured during this survey.

Experiment 2—Responses of Cerambycidae, Curculionidae: Scolytinae, to Lure Combinations That Included the *H. halys* Lure

We captured *M. scutellatus*, *M. carolinensis*, *I. pini*, and *I. grandicollis* in numbers sufficient to conduct statistical analyses (i.e., species with a mean total per trap >1). *Halyomorpha halys* was captured in insufficient numbers to allow for meaningful statistical analysis. Estimated mean catches per trap based on hierarchical GLM are in Supp. Table S1 and for raw means of all species in Supp. Table S2.

Catches of *M. scutellatus*

We captured a total of 380 *M. scutellatus*, of which 179 (47%) were female and 201 (53%) were male. The greatest total numbers of both sexes were captured when either panel traps (23% of total trap capture) or funnel traps (28% of total trap capture) contained a combination of all lures (Fig. 3a and b). However, no difference was observed between traps containing all lures and traps without MSB, indicating this lure does not affect trap capture of *M. scutellatus*. Similar numbers of males were captured with the two full combination lures for both trap types (10 per panel trap, 8 per funnel trap; $F_{1,35} = 1.63$; $P = 0.209$), but more females were captured in funnel traps than in panel traps with full lures (7 per panel trap, 12 per funnel trap; $F_{1,32} = 15.54$; $P \leq 0.001$). The combination bark beetle lure (I+LI) increased catches of both females (1.4/trap; $F_{1,32} = 39.34$; $P < 0.001$) and males (4.6 per trap; $F_{1,35} = 34.82$; $P < 0.001$) of *M. scutellatus* over catches with AE alone (0 per trap). The I+AE combination captured more *M. scutellatus* than the LI+AE treatment ($F_{1,35} = 10.93$, $P = 0.002$ for males; $F_{1,32} = 5.30$, $P = 0.028$ for females). The MSB lure was not attractive to *M. scutellatus* on its own and had no effect on trap capture in panel traps ($F_{1,35} = 2.85$, $P = 0.101$ for males; $F_{1,32} < 0.1$; $P > 0.99$ for females) when added to the combination of all other components.

Catches of *Monochamus carolinensis*

We captured a total of 116 *M. carolinensis*. Increases in *M. carolinensis* trap captures occurred when I ($F_{1,36} = 33.25$; $P < 0.001$) or LI ($F_{1,36} = 16.86$; $P < 0.001$) was added to AE (Fig. 3c). Catches were higher for traps baited with AE+I compared to traps with the lures AE+LI (1.1 per trap cf. 0.4 per trap; $F_{1,36} = 5.96$; $P = 0.020$). Adding M to AE+I+LI doubled the number of *M. carolinensis* captured (3.5 per trap cf. 1.4 per trap; $F_{1,36} = 9.30$; $P = 0.004$). Funnel traps baited with all lures captured more *M. carolinensis* (38% of total trap capture) than panel traps with all lures (6.8 per trap cf. 4.0; $F_{1,36} = 5.21$; $P = 0.028$) (Fig. 3c). The addition of the MSB lure to the beetle attractants had no effect on *M. carolinensis* trap captures in panel traps (4 per trap with the MSB lure cf. 3.5 per trap without; $F_{1,36} < 0.1$; $P > 0.99$), indicating the MSB lure had neither a negative nor a positive effect on catches of *M. carolinensis*. We captured no *M. carolinensis* in traps containing only AE or the MSB lure.

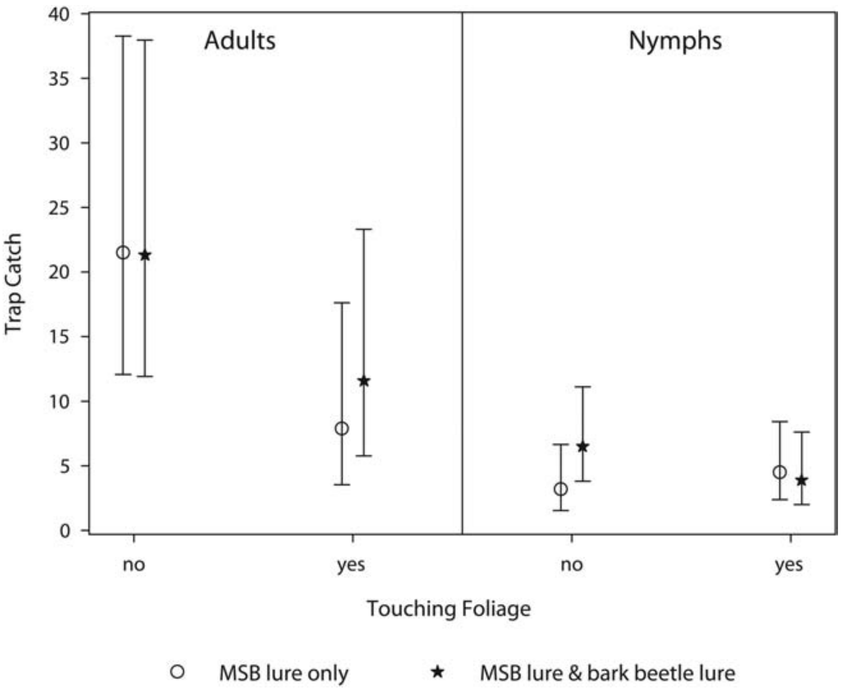

Fig. 2. Estimated mean trap capture (based on a hierarchical generalized linear model) of *Halyomorpha halys* adults and nymphs in modified panel traps. Traps were baited with the MSB lure (bisaboladienols & MDT; see text) with or without a blended bark beetle lure (see text) and either touching or not touching foliage. Error bars show 95% confidence limits.

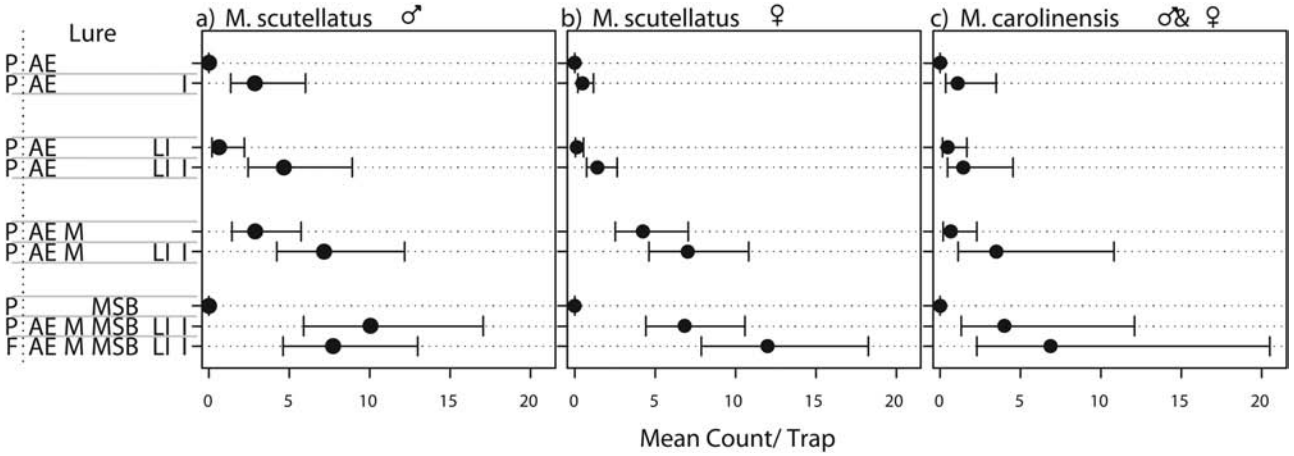

Fig. 3. Estimated mean trap capture (based on a hierarchical generalized linear model) of *Monochamus scutellatus* (male [a] and female [b]) and *M. carolinensis* (c) per trap baited with each combination of lures. Trap types: P, panel trap; F funnel trap. Lures: AE, α-pinene/ethanol; M, monochamol; LI, lanierone/ ipsdienol; I, ipsenol; MSB, *H. halys* attractant. See Table 1 for more explanation of the lure codes. Error bars show 95% confidence limits.

Catches of *I. pini*

We captured 2,416 *I. pini*, of which 1,514 (63%) were female and 902 (37%) were male. When all lures were present, catches of *I. pini* females were about 25% lower in funnel traps than in panel traps ($F_{1,34}$ = 4.49; P = 0.041; catches of 62/panel trap cf. 47/funnel trap) whereas catches of *I. pini* males were 60% greater in funnel traps than in panel traps ($F_{1,33}$ = 11.31; P = 0.002) (Fig. 4a and b). Trap captures of females and males increased significantly when the *I. pini* pheromones LI were added to either AE alone (males: $F_{1,33}$ = 91.31; P < 0.001; females $F_{1,34}$ = 69.43; P < 0.001), or AE+I (males: $F_{1,33}$ = 99.28; P < 0.001; females: $F_{1,34}$ = 69.68; P < 0.001) (Fig. 4a and b). The addition of M to the combination of AE+I+LI approximately halved trap captures for both female ($F_{1,34}$ = 14.31; P < 0.001) and male ($F_{1,33}$ = 25.80; P < 0.001) *I. pini*. We captured no *I. pini* with the lure combination of AE+M or with the MSB lure alone.

Catches of *I. grandicollis*

We captured 467 *I. grandicollis*. Traps baited with AE+I captured more *I. grandicollis* (44% of total trap capture) than traps with any other treatment ($F_{1,33}$ from 69.2 to 141; P < 0.001 for each comparison) (Fig. 4c). Among the other treatments, the highest catches occurred in funnel traps with the full lure combination and with the I+LI+AE combination (both 10.7 per trap), followed by the full lure combination in the panel trap and the combination of I+LI+AE+M (7.6 and 7.3 per trap) (Fig. 4c). No *I. grandicollis* were captured in

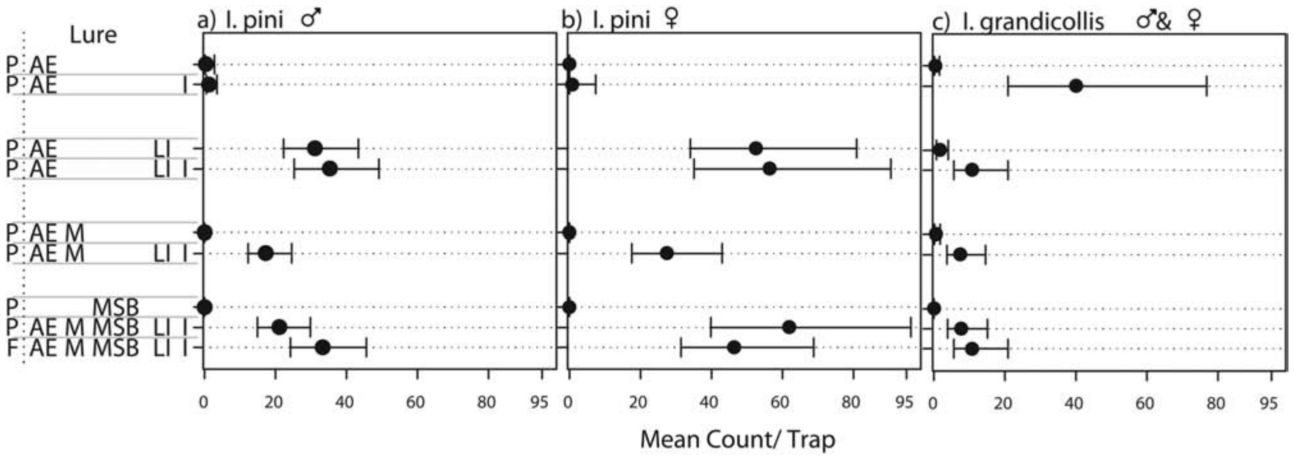

Fig. 4. Estimated mean trap capture (based on a hierarchical generalized linear model) of *Ips pini* (male [a] and female [b]) and *I. grandicollis* (c) per trap baited with each combination of lures. Trap types: P, panel trap; F funnel trap. Lures: AE, α-pinene/ethanol; M, monochamol; LI, lanierone/ipsdienol; I, ipsenol; MSB, Bisaboladienols & MDT. See Table 1 for more explanation of the lure codes. Error bars show 95% confidence limits.

traps containing only the MSB lure, and the addition of the MSB lure to the full combination of lures had no negative effect on trap capture ($F_{1,33} < 0.1$; $P > 0.99$ for both funnel and panel traps).

Catches of *H. halys*

We captured only 17 *H. halys* during this experiment. Most were trapped in the funnel traps with all lures (1.5 per trap; nine total insects trapped in six traps) (Supp. Table S1).

Discussion

We found that *H. halys* trap captures were not affected by the addition of bark beetle pheromones (experiment 1), and *Ips* spp. and *Monochamus* spp. trap captures were not affected by the addition of the *H. halys* attractants bisaboladienols and methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate (the MSB lure) (experiment 2). Agencies concerned with detecting *H. halys* could add the MSB lure to any existing surveillance programs targeting the beetle species tested here. These results suggest that agencies could reduce the total number of traps deployed in a multi-species surveillance program, therefore reducing costs while not decreasing the likelihood of trapping and detecting new incursions of the species targeted here.

Both *M. scutellatus* and *M. carolinensis* appear to be opportunistic species that respond to a variety of beetle pheromones and primary attractants that indicate recently killed trees suitable for colonization. Our findings conformed to those of Miller et al. (2016) for *M. carolinensis*, although they found that adding ipsenol to monochamol did not increase capture of *M. scutellatus*. However, the addition of bark beetle pheromones increased trap capture of *M. carolinensis*. Another study by Macias-Samano et al. (2012) showed that captures of *M. scutellatus* in traps baited with α-pinene, ethanol, ipsenol, and ipsdienol were no different from trap captures in traps baited with just α-pinene and ethanol. Allison et al. (2013) found that *M. carolinensis* trap captures were highest when ipsenol, ipsdienol, and *cis*-verbenol were used together. The pheromone *cis*-verbenol, which is produced by various species of bark beetles, was found to increase catches of *M. scutellatus* (de Groot and Nott 2004). In the current study, the addition of bark beetle pheromones, especially ipsenol, always increased trap captures of both *Monochamus* spp.

Attraction of *Monochamus* spp. outside of North America to bark beetle pheromones differs among species and regions. In Spain, Sweden, and Austria, the greatest number of *M. sutor* were captured when ipsenol was paired with monochamol (Pajares et al. 2017). In China, *M. alternatus* is attracted to monochamol in combination with ethanol and α-pinene (Teale et al. 2011), but it is not attracted to ipsenol or ipsdienol (Fan et al. 2010). *M. galloprovincialis* trap catches were highest in Spain and Italy when ipsenol, α-pinene, 2-methyl-3-buten-2-ol, and monochamol were combined (Pajares et al. 2010, Rassati et al. 2012). For all surveillance programs aimed at detecting *Monochamus* spp., it appears that combining the bark beetle lures ipsenol and ipsdienol with the combination of monoterpenes and monochamol provides the best opportunity to detect these insects.

Unlike *Monochamus* spp., which were captured in traps baited with bark beetle pheromones, *I. grandicollis* and *I. pini* responded to traps only when their own pheromones were present (Fig. 4). These results are consistent with field experiments conducted by Erbilgin and Raffa (2001), who showed that *I. pini* and *I. grandicollis* avoided each other when adult beetles were introduced to billets infested with the competitor. Miller et al. (2005) also showed *I. grandicollis* was not attracted to traps baited with lanierone and ipsdienol, and *I. pini* was not attracted to traps baited with ipsenol.

Various combinations of ipsenol with primary and secondary compounds affect trap captures of *I. grandicollis* in different ways. In the southeastern United States, *I. grandicollis* is not attracted to ethanol alone but is attracted to α-pinene. However, ethanol did not decrease trap catches when paired with α-pinene (Miller and Rabaglia 2009). Also in the southeastern United States, *I. grandicollis* was much more attracted to the combination of ipsenol and ipsdienol than to the combination of ethanol and α-pinene, and these primary attractants had a negative effect when paired with the pheromones (Miller et al. 2011). When primary attractants were not included, Miller et al. (2005) found that trap captures were not negatively affected by the addition of lanierone and ipsdienol to ipsenol in the southeastern United States. Allison et al. (2012) found that adding ipsdienol to ipsenol increased catches of *I. grandicollis* in Louisiana and Georgia. In the same study, the addition of *cis*-verbenol (a pheromone of the intraguild competitor *Ips calligraphus* Germar) did not affect trap captures negatively when added to ipsenol and ipsdienol. Catches of *I. grandicollis* in traps baited with monochamol, α-pinene, and ipsenol were similar to catches in traps baited with just α-pinene and ipsenol in Michigan, Georgia and South Carolina (Miller et al. 2016). Our present study contrasts with previous work in one way: we observed reduced trap capture of *I. grandicollis* when ipsdienol and lanierone were added to ethanol, α-pinene and ipsenol. However, no additional negative effects were observed when monochamol or the mix of bisaboladienols and methyl (*E,E,Z*)-2,4,6-decatrienoate were added. Although the full combination of lures did not catch the greatest number of *I. grandicollis*, they could still be detected in traps with the full complement of lures used in a surveillance program.

The effect of primary attractants on *I. pini* trap capture varies between geographic areas and is affected by release rates (Lanier et al. 1972, Miller et al. 1997). In this study, we found that male and female *I. pini* were not attracted to traps baited with α-pinene, ethanol and ipsenol, but were attracted to traps baited with α-pinene, ethanol, ipsdienol, and lanierone. In British Columbia, Canada, the monoterpene ß-phellandrene synergized attraction of *I. pini* to the pheromone ipsdienol more than other monoterpenes (3-carene, ß-pinene, limonene, α-pinene, myrcene, and terpinolene) (Miller and Borden 1990). In Wisconsin, Erbilgin and Raffa (2000) found that the addition of 3-carene to ipsdienol-baited traps increased catches of *I. pini* more than (-)-α-pinene, (+)-α-pinene, ß-pinene, and myrcene. These studies highlight that a wide array of different monoterpenes could be considered further for implementation into a multi-lure surveillance program for more robust detection.

Responses of *I. pini* to lanierone varies geographically in North America. For example, when ipsenol was paired with ipsdienol in North Carolina, a negative *I. pini* response was observed, but the addition of lanierone offset this effect (Miller et al. 2005). However, another study in Wisconsin revealed no negative response of *I. pini* trap capture from the pairing of ipsenol and ipsdienol without lanierone (Ayres et al. 2001). Also in Wisconsin, Aukema et al. (2000) found that *I. pini* was not attracted to the enantiomeric composition of 3% (+) / 97% (-) ipsdienol when lanierone was absent; the addition of lanierone increased catches of *I. pini* with all ipsdienol enantiomeric ratios in the same study. The geographic variation in the effects of lanierone on trap captures of *I. pini* was exemplified by the findings of Miller et al. (1997) who showed a synergistic response in *I. pini* catch in traps in eastern populations, but less so in western populations. Because of this geographic variation, we suggest using racemic blends of both ipsdienol and ipsenol in surveillance programs based on our results from experiment 2.

Bark beetle semiochemicals had no negative effect on trap capture of *H. halys* in experiment 1, and all *H. halys* captured in experiment 2 occurred in traps with all lures present. The high capture rate of *H. halys* adults by traps placed in open space rather than touching foliage (experiment 1) indicates that the modified panel trap is a viable surveillance tool for this insect, especially when placed away from foliage in open space. The relatively low capture of *H. halys* nymphs in experiment 1 reflects the trapping time period (October and November) when abundance of immature *H. halys* declines (Khrimiam et al. 2008). This study revealed how mobile immature *H. halys* are by their ability to climb across limbs and down ropes to find their way into suspended traps. Their ability to walk significant distances has previously been documented elsewhere (Lee et al. 2014). Experiment 2 was conducted early in the season (May and June) and low abundance of *H. halys* captured in traps confirms that lures for adult *H. halys* are not particularly attractive at this time and that nymphs were not yet present (Leskey et al. 2013). Nevertheless, our observation in experiment 2 that the majority of *H. halys* were found in funnel traps with all lures combined suggests that further research needs to be conducted to compare the efficacy of these traps with those of the standard pyramid and panel traps typically used to monitor this insect (Leskey et al. 2015). Regardless, pheromone-based monitoring for *H. halys* has been tested in its native host range, demonstrating its usefulness for surveillance programs (Morrison III et al. 2017).

Although we used only panel and funnel traps in the experiment, a range of other surveillance traps are available. Dodds et al. (2015) compared funnel traps, intercept panel traps and an aerial canopy malaise trap (i.e., a SLAM trap) and found that the SLAM trap was the most effective at capturing Cerambycidae. Here, we found that funnel and modified-panel traps paired with all lures captured about the same number of bark beetles and longhorn beetles, a similar result to that in Miller et al. (2013b) and Kerr et al. (2017). Other studies have found that panel traps capture more Cerambycidae (Graham et al. 2012). Further research could compare the standard surveillance traps (i.e., panel and funnel traps) against nontraditional traps (e.g., SLAM traps) for their efficiency in capturing many species across different orders.

Our results provide evidence that the compounds α-pinene, ethanol, ipsenol, lanierone, ipsdienol, monochamol, and a mix of bisaboladienols and methyl (*E,E,Z*)-2,4,6-decatrienoate could be used in combination to simultaneously monitor for *Ips* spp., *Monochamus* spp. and *H. halys*, increasing the efficiency of current surveillance programs. Although not measured here, this range of lures is also likely to detect a wider range of bark and wood-boring beetles, adding further benefits to this surveillance tool. However, further research should be conducted on the deterrent or attractive effects of these lures before any recommendation is given for any additional genus or species. A range of additional primary and secondary compounds exist; therefore, future research could focus on how additional compounds interact with the compounds tested here, to reduce costs further and increase detection capabilities.

Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

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