

Interaction of Visual and Chemical CUES in Promoting Attraction of *Agrilus planipennis*

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Abstract Female emerald ash borers, *Agrilus planipennis* (Coleoptera: Buprestidae), emit a macrocyclic lactone, (Z)-3-dodecen-12-olide, that increases field trap captures on large-panel prism traps when co-emitted with the green leaf volatile (Z)-3-hexenol. We assessed attraction to these compounds by using visual decoy-baited branch traps, which attract males by mimicking a living female resting upon a leaf. Pairs of branch traps, with and without visual decoy beetles, were placed on green ash, *Fraxinus pennsylvanica*, trees, which were assigned different odor treatments: 1) no odor, 2) (Z)-3-hexenol alone, and 3) (Z)-3-hexenol-plus-lactone. Male captures were positively affected by the presence of decoys and the emission of either (Z)-3-hexenol or (Z)-3-hexenol plus lactone. The decoy-baited traps with the combination of (Z)-3-hexenol plus lactone caught more males than any other treatment. Greater male captures were associated with continuing captures later in the season, suggesting that decoy and odor attractants remain attractive throughout the flight period. Female captures were not affected by the visual decoys, but odors did influence captures, with the (Z)-3-hexenol plus lactone treatment catching the greatest number of

females. The rare female trap captures were negatively correlated with the more common male captures on the odorless and (Z)-3-hexenol-baited traps, but were not correlated with male captures when the lactone was added. Thus, in the absence of the lactone, the visual signal of other conspecifics can inhibit female attraction. However, the pheromone attracts both sexes independently of the visual signal on the trap.

Keywords Emerald ash borer · Flight · Lactone · Invasive species · Mate search · Trapping · Coleoptera · Buprestidae

Introduction

The emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), has been a severe forest and urban pest since its accidental introduction to North America (Cappaert et al. 2005; Haack et al. 2002). An important component of *A. planipennis* management in North America is the development and application of effective methods for detecting pest populations. During the past ten years, there has been an intense effort to improve detection tools for this species, which is a member of an insect family that, historically, has received little attention for applied research (MacQuarrie et al. 2015; Silk and Ryall 2015). Potential visual and chemical attractants have been tested experimentally, revealing many of the cues used by *A. planipennis* for mate- and host-finding (Bartelt et al. 2007; Domingue et al. 2013a, 2015; Lelito et al. 2007, 2008, 2009; Silk et al. 2009, 2011). However, further research is necessary to provide a more complete understanding of the potential synergy of all relevant behavioral signals under field conditions.

Beyond cuticular hydrocarbon contact pheromones (Lelito et al. 2009; Silk et al. 2009), which would appear to have limited utility for trapping applications, there have been two

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types of chemical attractants developed for *A. planipennis*. The first includes plant-associated odors. *Agrilus planipennis* antennae are responsive to a number of *Fraxinus* bark odors (Crook et al. 2009) and common green leaf volatiles (DeGroot et al. 2008; Rodriguez-Saona et al. 2006). Attraction to standard green and purple “prism traps” (Francese et al. 2005, 2010) increased with the addition of commercially available bark distillates from species other than ash, such as manuka and phoebe oil, which share several volatile compounds with *Fraxinus* bark. Attraction also increased with the addition of the green leaf alcohol (*Z*)-3-hexenol (Grant et al. 2010, 2011). In these experiments, (*Z*)-3-hexenol consistently attracted more males than females to green or purple prism traps.

The second type of attractant that has been investigated is (*Z*)-3-dodecen-12-olide, the only known pheromone of a species in the Buprestidae. This lactone is produced primarily by females, and elicits antennal responses from both sexes (Bartelt et al. 2007). It was determined later that (*Z*)-3-dodecen-12-olide can enhance attraction of beetles to green prism traps, but only if co-emitted with (*Z*)-3-hexenol (Ryall et al. 2012, 2015; Silk et al. 2011, 2015). Furthermore, in ultraviolet light, (*Z*)-3-dodecen-12-olide isomerizes to (*E*)-3-dodecen-12-olide, which may also be attractive to male *A. planipennis* (Silk et al. 2011).

The visual signal of a quiescent *A. planipennis* beetle resting upon leaves in bright sunlight attracts males (Lelito et al. 2007) and, to a lesser degree, females (Domingue et al. 2015). Experiments have determined that dead pinned specimens, free of all volatile semiochemicals by previous washings with organic solvents, elicit stereotypical mating approaches by flying feral males from at least 1 m above pinned “visual decoys” (Lelito et al. 2007). Trapping approaches based upon this behavior have been developed successfully by catching beetles approaching decoys placed upon adhesive-covered leaves or small green plastic cards (5 × 9 cm) with wavelength emissions mimicking those of ash leaves (Domingue et al. 2013a, b; Lelito et al. 2008). Traps have been modified further by using synthetic decoys on sticky surfaces (Domingue et al. 2015) or with electricity that stuns males that land on the decoys (Domingue et al. 2014).

Here, we tested different volatile attractant blends coupled with a trap that exploited male visual mate-finding cues, in an attempt to optimize trapping efficacy for this invasive pest. The stimuli we used included: 1) (*Z*)-3-hexenol; 2) (*Z*)-3-hexenol plus the lactone pheromone; and 3) visual decoy beetles. The relative effects of these stimuli were examined by their independent addition to small “branch traps” that provided green plastic surfaces placed within a tree to mimic the normal foliar mating environment (Domingue et al. 2013a, 2015). We thus assessed, under field conditions, which of these visual and chemical attractants was of primary importance, and whether their effects were synergistic.

Methods and Materials

Field Site Traps were deployed on May 25, 2015 at a site on the Pennsylvania State University campus in University Park, PA, USA (40°48'31.5"N 77°50'25.1"W, 318 m altitude). The predominant tree species on this site is green ash, *Fraxinus pennsylvanica* Marsh, which was planted uniformly in 1978 (Steiner et al. 1988). The ca. 2000 trees planted at this site were spaced in rows and columns that were separated by 3.7 m. By the time of the experiment in 2015, most trees were experiencing mortality or serious signs of decline, including crown dieback and epicormic sprouting.

Branch Traps For trapping, 24 trees were selected that had not yet experienced complete crown dieback. This meant that there were some living branches producing foliage that had existed before infestation began. It was important that all selected trees had living branches that terminated less than 2 m from the ground to facilitate placement and inspection of traps. These branches also were suitable for trap deployment because they were exposed to direct sunlight during some part of the day, which provides conditions that, as observed in past experiments, promote optimal male attraction to decoys (Lelito et al. 2007) and pheromone (Ryall et al. 2015).

Branch traps have been used and described in detail for previous studies (Domingue et al. 2013b, 2015). The frame of each branch trap consisted of two green sticky plastic rectangles (5 × 9 cm) stapled to an inverted white delta trap (ISCA Technologies, CA, USA). The cards were cut from a highly reflective green plastic material with peak reflectance of ca. 60 % at 535–540 nm, identical to that used in prism traps in previous studies (Crook et al. 2009). The reflectance of the material across the visual spectrum is provided in a previous publication concerning branch traps (Domingue et al. 2015). The material was obtained from ChemTica Internacional (Heredia, Costa Rica). The green sticky cards took on an A-frame configuration, with both surfaces of the dual cards oriented toward the sun, ca. 45° relative to the ground (Suppl. Figure 1). Each trap was slipped over a leaf-and-branch cluster, and fastened with spring-hinged clips to the leaves.

Visual and Olfactory Stimuli On each of the trees selected for the experiment, two of the traps described above were affixed ca. 1–2 m apart. On each tree, one of the dual-surface traps was provided with visual decoys while the other was not. The visually baited traps were provided with female *A. planipennis* specimens pinned to the center of each card. The green plastic surfaces of the traps, including decoys, then were sprayed with a thin coating of Tanglefoot™ (The Tanglefoot Company, Grand Rapids, MI, USA). Dead *A. planipennis* specimens, used as visual decoys, were provided by the APHIS rearing facility in Brighton, MI, USA.

One of three odor treatments was assigned to each of the 24 trees selected. The two traps placed on each tree (visual decoy-free and visual decoy-baited), always were provided the same odor treatment, or no odor at all, in order to test the interaction between visual and chemical cues. The first odor treatment was an odor-free control. The second was (*Z*)-3-hexenol alone, consisting of (*Z*)-3-hexenol packets (Synergy Semiochemicals Burnaby, B.C., CA) attached to the interior of the open delta trap, both for visual decoy-free and visual decoy-baited branch traps placed on a tree. The release rate of (*Z*)-3-hexenol from each packet was ca. 40 mg/day, measured by weight loss. Thus, odor emanated from the trap at a height just below the green sticky-card surfaces (Suppl. Figure 1B). The odor treatment for the remaining one third of traps consisted of a combination of (*Z*)-3-hexenol and the lactone pheromone. For this treatment, the aforementioned (*Z*)-3-hexenol packets again were clipped inside the branch trap but, in addition, a red rubber septum loaded with 3.0 mg of the lactone pheromone, emitted at ca. 60 µg/day at 25 °C, also was fastened to the (*Z*)-3-hexenol pouch, such that it was exposed to air flow ca. 3 cm below the green surfaces of the cards.

So that variation in localized abundance of beetles and other unique tree effects were minimized, two additional precautions were taken with respect to experimental design. First, traps were placed so that different odor treatments always were assigned to trees close to one another (Suppl. Figure 2). Furthermore, within clusters of nearby trees, traps were rotated twice after their initial May 25 deployment: on June 20 and July 5. Using this protocol, each tree in the experiment was assigned to each of the three treatment groups for one time period during the course of the experiment. We also replaced beetle decoys on each trap when they were rotated, because beetles often darken after prolonged exposure to sunlight.

Handling of Specimens All traps were checked daily, with buprestids removed from each trap being placed in plastic bags for later identification. Only buprestid beetles were saved, with other non-target insects being discarded. Specimens were frozen (for up to 3 mo) before the Tanglefoot glue was removed, so that species and sexual identities of all *A. planipennis* could be confirmed. To remove the Tanglefoot glue, the specimens were placed in Histo-Clear (National Diagnostics, Atlanta, GA, USA) for 24 h, and then successively rinsed with hexane, acetone, and ethanol. Although nearly all buprestids were *A. planipennis*, a handful of specimens of other species, including *Agrilus cyanescens* Ratzeburg and *Agrilus subcinctus* Gory, also were caught, but these were too few to be considered in any analysis. All *A. planipennis* specimens were examined further by dissecting genitalia to confirm sex.

Statistical Analyses Analysis of variance was performed to evaluate the effects of decoy presence and odor treatment (2×3 factorial design). We also included a factor in the model, *Day*Tree(Odor)*, which considered the interaction of the day of the trapping event with the individual tree upon which each odor treatment was deployed. This interaction effect was used as the error source for ANOVA. The model was applied separately for male and female *A. planipennis* captures. Pearson correlations between daily male and female captures were calculated separately within each decoy and odor treatment combination. Proc GLM and Proc CORR in SAS version 9.2 2008 (SAS institute, Cary, NC, USA) were used for these calculations.

We also were interested in potential phenological factors that affect trap captures. Thus, we compared the average date on which each male or female *A. planipennis* landed upon the trap, within each decoy and odor treatment combination. As observed in past trapping experiments (Domingue et al. 2015), seasonal trap captures of beetles had a multimodal distribution. Within each treatment, the dates of capture of *N* specimens were re-sampled with replacement *N* times in each of 10,000 replicates to provide 95 % bootstrap confidence intervals. Confidence intervals for the differences of resampled means of each of the 15 possible comparisons of treatment means also were calculated. To correct for experiment-wise error, a conservative Bonferroni adjustment was performed, evaluating 99.67 % confidence intervals of the distribution of differences between the bootstrapped means, to obtain comparisons at $\alpha = 0.05$.

Results

During the first few days of the trapping experiment, there was a small peak in male capture, which was similar in magnitude for all odor and visual decoy treatments (Fig. 1). All experimental treatments had their greatest captures near June 20. In some treatments, another peak was distinguishable around July 12. This later peak was associated with traps that had been baited with either visual decoys or lactone pheromone (Fig. 1 b,d,e,f).

Analysis of variance demonstrated effects of odor treatment and decoy presence on male trap captures (Table 1), with more beetles caught in visual decoy-baited traps with (*Z*)-3-hexenol-plus-lactone than in all other treatments without one or more of these stimuli (Fig. 2a). The male catch was roughly twice as great when all of these attractants were used together compared to any of the other treatments.

The late season trap capture of males, which was common for some treatments (Fig. 1), contributed to differences in average date of trap capture (Fig. 2b). Visual decoy-baited traps with (*Z*)-3-hexenol, or (*Z*)-3-hexenol plus lactone (with or without decoys), had similar average dates on which males

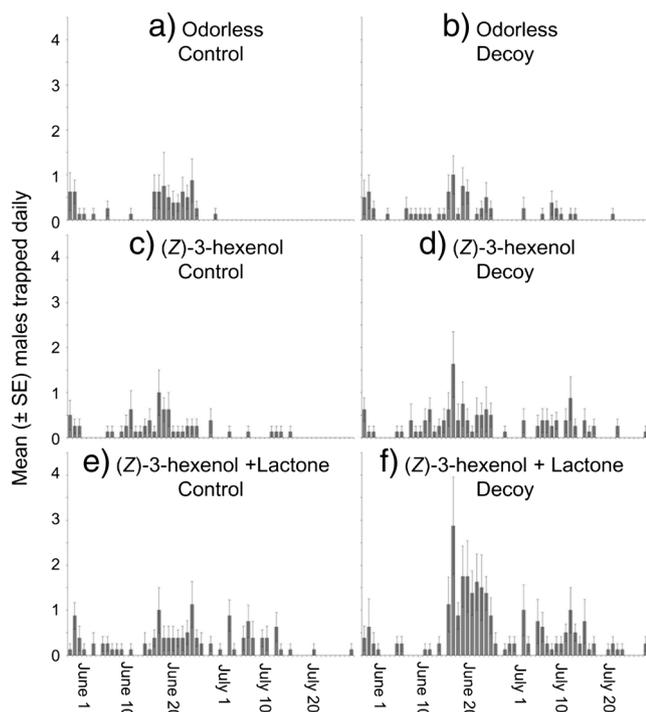


Fig. 1 Mean (\pm SE) capture of adult male *Agrilus planipennis* on traps of each treatment for every day throughout the season in six experimental treatments including **a** odorless without a decoy, **b** odorless with a decoy, **c** (Z)-3-hexenol-baited without a decoy, **d** (Z)-3-hexenol-baited with a decoy, **e** (Z)-3-hexenol and lactone-baited without a decoy, and **f** (Z)-3-hexenol and lactone-baited with a decoy

were captured, ranging from June 24–26. However, visual decoy-free traps that were either odorless or baited only with (Z)-3-hexenol, had earlier mean male capture dates ranging from June 15–17. Odorless, visual baited-traps had a mean capture date near June 18, which was not different from either group. Thus, the observed increase in attraction of males to the decoy and pheromone baited traps was at least partially associated with these traps continuing to capture males later in the season.

There were far fewer females ($N = 92$) than males ($N = 620$) captured during the course of the trapping experiment.

Table 1 Analysis of variance for adult male and adult female *Agrilus planipennis* captures

	Source	DF	Type III SS	Mean Square	F	P
Males	Day ^a Tree(Odor)	1245	764	0.614		Error source ^a
	Odor	2	22.9	11.5	18.69	< 0.001
	Decoy	1	10.3	10.3	16.71	< 0.001
	Odor ^a Decoy	2	5.54	2.77	4.51	0.011
Females	Day ^a Tree(Odor)	669	55.9	0.0836		Error source ^a
	Odor	2	0.760	0.380	4.55	0.011
	Decoy	1	0.0476	0.0476	0.57	0.451
	Odor ^a Decoy	2	0.260	0.130	1.56	0.212

^a For both males and females, the tree by date variance was used as the error term for a 2×3 factorial analysis of odor and decoy effects

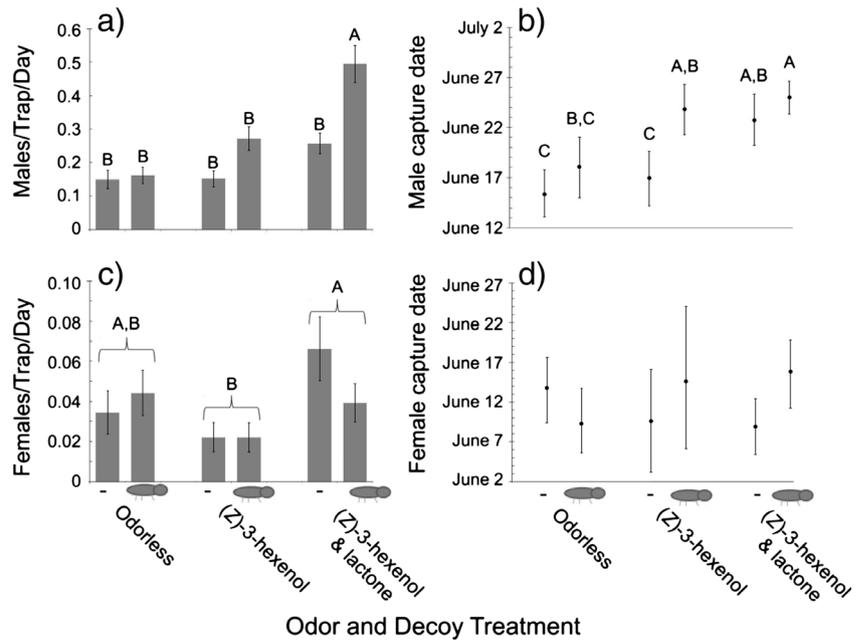
Defined peaks in catch were not as readily apparent as they were for males (Fig. 3). Female captures occurred sporadically and earlier in the season, usually before July 1. The odor treatment had an effect on female trap capture, but the presence of decoys did not (Table 1). More females were caught on traps baited with (Z)-3-hexenol plus lactone than on those baited with only (Z)-3-hexenol (Fig. 2c). Odorless traps were of intermediate effectiveness. There were no effects of either odor or decoy upon date of female trap capture (Fig. 2d).

Within the odorless and (Z)-3-hexenol treatments, regardless of whether or not decoys were present, there were negative correlations between male and female captures (Table 1). However, in the (Z)-3-hexenol plus lactone-baited treatment, there was no correlation between the total number of males and females that were captured for both visual decoy- and non-visual decoy-baited traps (Table 2).

Discussion

The data indicate that visual decoys and volatile odor blends contribute to the attraction of male *A. planipennis* during field trapping. Although a positive effect previously was shown when (Z)-3-hexenol, phoebe oil or manuka oil was added to decoy traps for *A. planipennis* (Domingue et al. 2013a), it is apparent that the addition of lactone pheromone to (Z)-3-hexenol also enhances attraction to decoy traps. This experiment demonstrated that any optimal formulation for branch traps should include the presentation of visual decoys, (Z)-3-hexenol, and the lactone pheromone. Comparing decoy-baited branch traps by using only (Z)-3-hexenol against those with addition of the pheromone to (Z)-3-hexenol, there was an 82 % increase in trap capture of *A. planipennis* males in the latter. Without visual decoys, the (Z)-3-hexenol plus lactone-baited traps had an 86 % increase in catch relative to traps baited with (Z)-3-hexenol. These increases are within the range that were found in prism trap captures when the lactone pheromone was added alongside (Z)-3-hexenol (Ryall et al. 2012, 2015; Silk et al. 2011, 2015).

Fig. 2 Mean (\pm SE) daily captures and mean (\pm 95 % bootstrap CI) date of capture of adult males (**a, b**) and females (**c, d**) *Agrilus planipennis* within each of the six decoy and odor treatments. For daily capture rates, different letters indicate differences among means ($P < 0.05$, using Tukey adjustment). For male capture rates, all treatments were considered separately, but for female captures, the decoy treatments were pooled because the effect was not significant (Table 1). For male capture dates, different letters indicate differences among means ($P < 0.05$, Bonferroni adjustments respectively). Female capture date showed no differences among treatments



Although visual decoys increased male captures when added to odor baits, it was not expected that decoys would have such a small effect on male catch when added to odor-free traps. In previous *A. planipennis* trapping experiments that included treatments in which no odor lures were provided,

there were significant and consistent increases in trap captures when decoys were added to traps (Domingue et al. unpublished; Lelito et al. 2008). Failure to observe such an effect might be the result of unintended odor interactions between the traps. More specifically, those males that were more actively seeking mates may have bypassed trees on which no supplemental odors were added in order to search for mates on nearby trees baited with volatile attractants. Thus, most males on traps on control trees simply may have been males approaching foliage for feeding and incidentally landing upon branch traps.

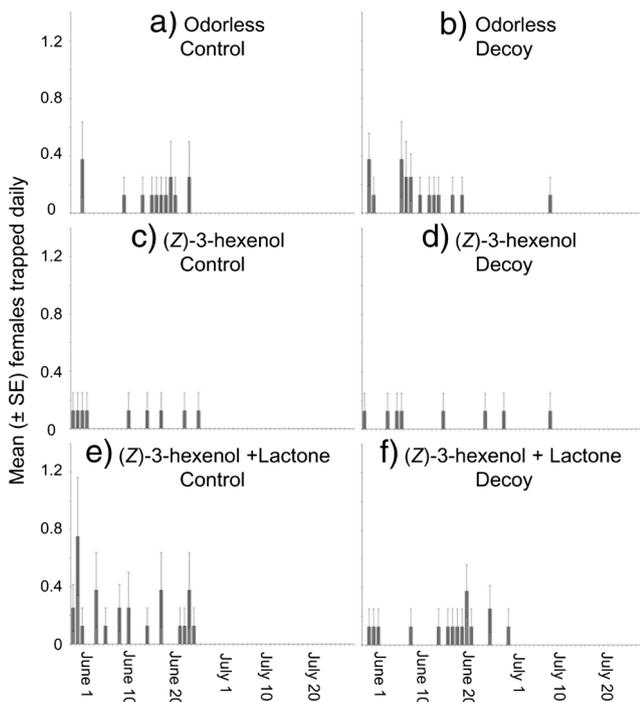


Fig. 3 Mean (\pm SE) capture of adult female *Agrilus planipennis* on traps for every day throughout the season in six experimental treatments, including **a** odorless without a decoy, **b** odorless with a decoy, **c** (Z)-3-hexenol-baited without a decoy, **d** (Z)-3-hexenol-baited with a decoy, **e** (Z)-3-hexenol and lactone-baited without a decoy, **f** (Z)-3-hexenol and lactone-baited with a decoy

The number of females caught in this experiment was much lower than the number of males and, consequently, it was more difficult to elucidate and interpret the phenological and behavioral factors that influenced capture of females. In a previous experiment, females were caught at a higher rate on similar branch traps when decoys were added, although they typically were caught further away from the visual decoys on

Table 2 Pearson correlations between adult male and adult female *Agrilus planipennis* captures within each of the odor and decoy treatments applied to the branch traps

Odor	Decoy	Correlation Coefficient
Odorless	Absent	-0.342**
	Present	-0.469*
(Z)-3-hexenol	Absent	-0.482*
	Present	-0.428*
(Z)-3-hexenol and lactone	Absent	-0.034
	Present	0.090

*The correlation coefficient is significant at $\alpha = 0.05$

**The correlation coefficient is marginally significant at $\alpha = 0.1$

the sticky surfaces than were males (Domingue et al. 2015). Furthermore, in another trapping experiment, simply using a background of a single ash leaflet, a much smaller background for the visual decoy, decoys had a negative impact on female capture rate (Lelito et al. 2008). In the current study, there was a negative correlation between female and male captures in the absence of the lactone pheromone. This finding is consistent with previous experiments because it suggests that there can be positive or negative feedback to females from the visual signal of other beetles, depending on the uninhabited background space available to approaching females. Thus, when many male beetles were caught on traps, females became less likely to approach. However, in the current study, when (*Z*)-3-hexenol plus lactone was presented, there was no longer a negative relationship between male and female captures, despite very high rates of male captures (Figs. 1, 2). Thus, for female *A. planipennis*, the (*Z*)-3-hexenol plus lactone cue may be more consistently attractive and take precedence over visual cues, which can change depending on beetle density and background. Thus, female-emitted pheromone seemed to encourage other females to join higher density aggregations of other *A. planipennis* that would otherwise be avoided when this signal is absent.

There are several implications of these findings for potential use of these small branch traps as an alternative to larger prism and funnel traps in some applications. Although visual-decoy baited traps could detect *A. planipennis* at as high a frequency as the larger prism traps at high population densities (Domingue et al. 2013a), branch traps have not yet been evaluated for *A. planipennis* detection at lower population densities. Given the results of this study and previous ones using prism traps (Silk et al. 2011), use of (*Z*)-3-hexenol and the lactone pheromone, (*Z*)-3-dodecen-12-olide, likely should provide an optimal attractive formulation for all traps potentially deployed for such a comparison. Additionally, branch traps might prove to be easier to use and more cost-effective if other low cost materials could be substituted. It already has been determined that inexpensive 3D-printed plastic models coated with green paint are durable and attract *A. planipennis* to traps as well as do real dead-beetle decoys, which deteriorate through the season (Domingue et al. 2015). Other increases in cost effectiveness may be attainable. For instance, experiments using prism traps have suggested that it may be possible to replace (*Z*)-3-dodecen-12-olide with a saturated analog (Silk et al. 2015). Thus, it would be useful to confirm similar efficacy of the branch traps with these alternative visual and chemical signals. A (*Z*)-3-hexenol plus lactone formulation also might increase the detection capabilities of visual decoy-based electric stun traps (Domingue et al. 2014), which have deployment advantages because they preclude the need for sticky glue. Such traps would require less maintenance, because there is no accumulation of “visual clutter” from non-target (and target) insects on the surfaces that

compromises the quality of the visual signal emitted by a single, attractive visual decoy.

More broadly, the current study advances our understanding of the synergistic effects of both visual and semiochemical cues produced by both this buprestid and its host plant. It is now clear that each of these factors plays a role in mate finding and host location in adult *A. planipennis*. Male attraction clearly is synergized by a combination of the decoy with (*Z*)-3-hexenol and lactone pheromone. Female responses remain difficult to elucidate, in part because of lower capture numbers, and perhaps also because of greater complexity of their behavioral repertoire. It also should be possible to manipulate characteristics of these signals under different field conditions with respect to population density and host condition to elucidate further the pertinent visual- and chemical-mediated behaviors in this species.

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