

Responses of Cerambycidae and Other Insects to Traps Baited With Ethanol, 2,3-Hexanediol, and 3,2-Hydroxyketone Lures in North-Central Georgia

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ABSTRACT In north-central Georgia, 13 species of woodboring beetles (Coleoptera: Cerambycidae: Cerambycinae) were attracted to multiple-funnel traps baited with ethanol and one of the following pheromones: (1) racemic 3-hydroxyhexan-2-one; (2) racemic 3-hydroxyoctan-2-one; and (3) *syn*-2,3-hexanediol. The following species were attracted to traps baited with ethanol and 3-hydroxyhexan-2-one: *Anelaphus pumilus* (Newman), *Eburia quadrigeminata* (Say), *Eudermes pini* (Olivier), *Knolliana cincta* (Drury), *Neoclytus mucronatus* (F.), *Neoclytus scutellaris* (Olivier), and *Xylotrechus colonus* (F.). *Clytus marginicollis* Castelnau & Gory, and *Anelaphus parallelus* (Newman) were attracted to traps baited with ethanol and 3-hydroxyoctan-2-one, whereas traps baited with ethanol and *syn*-2,3-hexanediol were attractive to *Anelaphus villosus* (F.), *A. parallelus*, *Neoclytus acuminatus* (F.), *Neoclytus jouteli jouteli* Davis, and *Megacyllene caryae* (Gahan). Ethanol enhanced catches of seven cerambycid species in traps baited with *syn*-2,3-hexanediol and 3,2-hydroxyketones. Catches of bark and ambrosia beetles (Curculionidae: Scolytinae) in ethanol-baited traps were largely unaffected by the addition of *syn*-2,3-hexanediol and 3,2-hydroxyketone lures, except for two species. The mean catches of *Hypothenemus rotundicollis* Wood & Bright and *Dryoxylon onoharaensum* (Murayama) in ethanol-baited traps increased and decreased, respectively, with the addition of racemic 3-hydroxyoctan-2-one. Traps baited with ethanol and *syn*-2,3-hexanediol were attractive to *Xylobiops basilaris* (Say) (Bostrichidae) and *Chariessa pilosa* (Forster) (Cleridae), whereas *Temnoscheila virescens* (F.) (Trogossitidae) were attracted to traps baited with ethanol and 3-hydroxyhexan-2-one. The assassin bug, *Apiomerus crassipes* (F.) (Hemiptera: Reduviidae), was attracted to traps baited with ethanol and 3,2-hydroxyketones.

KEY WORDS Cerambycidae, hardwood, detection, adventive, exotic

Concerns about new detection tools for adventive species of Cerambycidae (Coleoptera) that attack hardwood trees in North America began with the first infestations of the Asian longhorn beetle, *Anoplophora glabripennis* (Motschulsky), in Chicago and New York (Haack et al. 2010). Numerous introductions of *A. glabripennis* have occurred in eastern Canada and the United States over the past 20 years, with potential losses of >30% of urban trees in the United States (Nowak et al. 2001, MacLeod et al. 2002). Owing to a lack of an effective trapping system, detection of beetles was done by solely visual inspection of infested trees by tree climbers at a considerable cost. For the period 1996–2008, the costs of eradication efforts against *A. glabripennis* in Canada and the United States totaled >\$400 million (Haack et al. 2010).

Huge volumes of containerized goods shipped in solid-wood packaging continue to ensure that live,

woodboring insects arrive in new habitats (Haack et al. 2014). Early detection programs for adventive species of woodborers are critical in countering their impacts on native trees and forests. Early detection is one of four aspects of a management program for adventive species (Chornesky et al. 2005, Coulston et al. 2008, Klepzig et al. 2010, Liebhold et al. 2012). Detection programs in North America and overseas have typically targeted bark and ambrosia beetles, with traps baited with host volatiles such as ethanol and α -pinene (Grégoire and Evans 2007, Rabaglia et al. 2008, Jackson et al. 2010). Ethanol and α -pinene are broadly attractive to bark and woodboring beetles (Allison et al. 2004; Coyle et al. 2005; Miller 2006; Miller and Rabaglia 2009; Reding et al. 2011; Kelsey et al. 2013; Ranger et al. 2010, 2011, 2014). Similar broad-spectrum lures are required for a broad range of Cerambycidae associated with hardwood trees and shrubs that may be intercepted at ports-of-entry in North America and overseas (Allen and Humble 2002, Haack et al. 2014).

Structural motifs or chemical classes are known for various groups of insect pheromones. Lepidoptera typically use straight-chain carbon acetates, alcohols, and aldehydes as sex pheromones with polyene hydrocarbons and epoxides representing a second class of lepidopteran sex pheromones (Millar 2000). Compounds

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such as ipsenol, ipsdienol, and verbenols are common pheromones for bark beetles (Curculionidae: Scolytinae) (Borden 1982; Byers 1989, 2004). Similarly, a structural pheromone motif of alkanediols and hydroxyketones has been noted for many species of Cerambycidae in North America, particularly in the Cerambycinae (Allison et al. 2004, Ray et al. 2006, Hanks et al. 2007, Hanks and Millar 2013).

In Illinois, male *Xylotrechus colonus* (F.) produce racemic 3-hydroxyhexan-2-one, (2*S*,3*S*)-2,3-hexanediol, and (2*R*,3*R*)-2,3-hexanediol as an aggregation pheromone blend that attracts male and female *X. colonus* (Lacey et al. 2009). Lacey et al. (2009) found that traps baited with 2,3-hexanediols and 3-hydroxyhexan-2-ones also captured *Neoclytus acuminatus* (F.) and *Neoclytus mucronatus* (F.), respectively. Male *N. acuminatus* produce (2*S*,3*S*)-2,3-hexanediol (Lacey et al. 2004), whereas male *N. mucronatus* produce (3*R*)-3-hydroxyhexan-2-one (Lacey et al. 2007). In Illinois, Lacey et al. (2004) found that female *Curius dentatus* Newman were attracted to traps baited with a blend of the four stereoisomers of 2,3-hexanediol. The aggregation pheromone for *Megacyllene caryae* (Gahan) in Illinois consists of seven compounds that include (2*S*,3*R*)- and (2*R*,3*S*)-2,3-hexanediol in a 10:1 ratio (Lacey et al. 2008.). Male *Neoclytus scutellaris* (Olivier) in Illinois produce (*R*)-3-hydroxyhexan-2-one, and both sexes are attracted to traps baited with racemic 3-hydroxyhexan-2-one (Ray et al. 2015). Similarly, (*R*)-3-hydroxyhexan-2-one is an aggregation pheromone for *Anelaphus pumilus* (Newman), *Cyrtophorus verrucosus* (Olivier), *Eudercus pini* (Olivier), *Phymatodes aereus* (Newman), *Phymatodes amoenus* (Say), *Phymatodes lengi* Joutel, and *Phymatodes varius* (F.) in Illinois and Michigan (Mitchell et al. 2013, 2015). In California, *Anelaphus inflaticollis* Chemsak, *Phymatodes lecontei* (LeConte), and *Xylotrechus nauticus* (Mannerheim), use 3-hydroxyhexan-2-one as a pheromone (Hanks et al. 2007, Ray et al. 2009). In an extensive study conducted in Pennsylvania during 2009–2011, Hanks and Millar (2013) found 12 species of Cerambycinae attracted to traps baited with 2,3-hexanediols and 3,2-hydroxyketones.

Our goal was to broadly corroborate the attractiveness of traps baited with 2,3-hexanediols and 3,2-hydroxyketones for common cerambycid species found in forested habitats of north-central Georgia; habitats that are significantly different from those in California, Illinois, Michigan and Pennsylvania. Geographic variation in behavioral responses to pheromones is always a concern when dealing with insects (Borden et al. 1986, Miller et al. 1997, McElfresh and Millar 1999, Schlyter and Birgersson 1989, El-Sayed et al. 2003, Sorenson et al. 2005). Many northern species of cerambycids range into southeast United States, and confirmation of their response profiles over a broader geographic area should deter any concerns that managers of detection programs might have with variation in lure efficacy among locations. Moreover, we wanted to corroborate previous results by using commercially available lures that can last at least 3–4 wk without replacement. Managers of detection programs should prefer long-lasting lures that minimize servicing costs of traps.

One specific objective in this study was to determine the effect of ethanol on the responses of cerambycids to traps baited with hydroxyketones and hexanediols. Ethanol was commonly used as a diluent in 3,2-hydroxyketone and alkanediol lures in studies conducted in North America (Lacey et al. 2004, 2007; Hanks et al. 2007). Ethanol is emitted from stressed trees (Kelsey and Joseph 2003, Ranger et al. 2010, Kelsey et al. 2014) and enhances attraction of some species of bark and woodboring beetles to monoterpenes (Chénier and Philogène 1989; Miller and Rabaglia 2009; Sweeney et al. 2004, 2006, 2014). We predicted that ethanol would synergize attraction of longhorn beetles to traps baited with 3,2-hydroxyketone and 2,3-hexanediol lures, thereby increasing the efficacy of these lures in operational detection programs.

Another specific objective of our study was to evaluate the effects of 2,3-hexanediols and 3,2-hydroxyketones on catches of bark and ambrosia beetles commonly targeted with ethanol-baited traps in early detection programs for adventive species. Adding 2,3-hexanediols and 3,2-hydroxyketone lures to ethanol-baited traps used in current programs could help reduce costs associated with detection programs (Hanks et al. 2012, Noseworthy et al. 2012, Wong et al. 2012). We also noted trap catches of any other group of insects to these lures, particularly beetle predators. Beetle predators prey on adult and larval beetles and potentially could use 2,3-hexanediols and 3,2-hydroxyketones as kairomones to locate their prey.

Materials and Methods

In 2011–2013, we conducted three separate trapping experiments in coniferous and hardwood stands in the piedmont region of north Georgia with ethanol, 2,3-hexanediol and 3,2-hydroxyketone lures (Table 1). Contech Enterprises Inc. (Victoria, BC) supplied the following lures: Et – black, high-release rate ethanol pouch lures (20 mm by 45 mm by 335 mm); D6 – white pouch lures (4 mm by 85 mm by 110 mm) containing *syn*-2,3-hexanediol [50:50 mix of (2*R*,3*R*)- and (2*S*,3*S*)-2,3-hexanediol]; K6 – brown pouch lures (5 mm by 50 mm by 125 mm) containing racemic 3-hydroxyhexan-2-one; and K8 – brown pouch lures (5 mm by 50 mm by 125 mm) containing racemic 3-hydroxyoctan-2-one. The chemical purity of all compounds met or exceeded 95%. Each pouch lure (D6, K6, and K8) consisted of a cellulose sponge loaded with *syn*-2,3-hexanediol or one of the hydroxyketones, and sealed inside a polyethylene pouch (Sweeney et al. 2014). The release rate for ethanol was about 0.5 g/d at 23°C, whereas *syn*-2,3-hexanediol, 3-hydroxyhexan-2-one, and 3-hydroxyoctan-2-one were released at 1.5 mg/d, 25 mg/d, and 20 mg/d, respectively, at 20°C. All rates were determined gravimetrically by the manufacturer. We have found that *syn*-2,3-hexanediol and hydroxyketone lures last 3–4 wk in Georgia during summers with mean high temperatures of 30–35°C (unpublished results).

In each behavioral-choice experiment, we deployed 10-unit multiple-funnel traps (Contech Enterprises

Table 1. Locations, coordinates, dominant tree species, and trapping dates for each of three experiments on flight responses of wood-boring beetles to multiple-funnel traps baited with ethanol, *syn*-2,3-hexanediol, and 3,2-hydroxyketones in north-central Georgia

Exp	Location	Coordinates	Tree species	Trapping dates
1	Oconee National Forest, Putnam Co., GA	33.344 N, 83.457 W	<i>Quercus alba</i> L., <i>Quercus falcata</i> Michaux, <i>Liquidambar styraciflua</i> L., <i>Pinus echinata</i> Miller, <i>Carya tomentosa</i> Sargent	20 July–29 Sept. 2011
2	Rock Eagle, Putnam Co., GA	33.435 N, 83.389 W	<i>Pinus taeda</i> (L.), <i>P. echinata</i> , <i>L. styraciflua</i>	22 March–17 May 2012
3	Oconee National Forest, Putnam Co., GA	33.234 N, 83.521 W	<i>Q. alba</i> , <i>Q. falcata</i> , <i>L. styraciflua</i> , <i>P. taeda</i> , <i>P. echinata</i> , <i>Sassafras albidum</i> Presl	10 July–20 Aug. 2013

Inc.) in a randomized block design, spaced 10 m apart within and between replicate blocks. Each trap was modified by increasing the center hole of each funnel from 5 cm to 12 cm, thereby allowing placement of lures within the funnels (Miller et al. 2013). Traps were suspended between trees by rope such that each trap was >2 m from any tree and the bottom of each trap was 0.5–1.0 m above ground level. Each collection cup contained 150–200 ml of Splash RV & Marine Antifreeze (SPLASH Products Inc., St. Paul, MN) (a.i., propylene glycol) as a killing and preservation agent (Miller and Duerr 2008). Traps were deployed during the summer months for a period of approximately 8–12 wk, with catches collected every 2 wk and new antifreeze solution added on each occasion. Cerambycidae species were identified using Chemsak (1996) and Lingafelter (2007). Taxonomy followed Monné and Bezark (2013) and ITIS (2015). Voucher specimens of all species were deposited in the University of Georgia Collection of Arthropods (UGCA), Georgia Museum of Natural History, University of Georgia (Athens, GA).

We used 64 traps in Experiment 1, set in eight blocks of eight traps per block. One of the following treatments was randomly allocated to each of the eight traps within each block: 1) unbaited control (C); 2) D6; 3) K6; 4) K8; 5) Et; 6) Et + D6; 7) Et + K6; and 8) Et + K8. We used 40 traps in both Experiments 2 and 3, set in 10 blocks of four traps per block. In both experiments, one of the following four treatments was randomly allocated to each of the four traps within each block: 1) Et; 2) Et + D6; 3) Et + K6; and 4) Et + K8. 3,2-Hydroxyketone and *syn*-2,3-hexanediol lures were replaced after 3 wk in Experiment 1, and after 4 wk in Experiments 2 and 3.

In each experiment, statistical analyses were conducted on total cumulative numbers of insects captured per trap over the entire trapping period. Trap catch data were transformed by $\ln(Y+1)$ to ensure homoscedasticity (Pepper et al. 1997) for species with sufficient numbers of individuals ($N > 25$) captured. Normality and homoscedasticity were verified using the Shapiro-Wilk and equal variance tests, respectively, with the SigmaStat (ver. 3.01) statistical package (SYSTAT Software Inc., Point Richmond, CA). To ensure homoscedasticity in our analyses, treatments for some species were omitted from analyses when means and variances for a treatment in an experiment were both zero (Reeve and Strom 2004). In each experiment, trap catch data were subjected to ANOVA with the

SigmaStat package using the following model components: 1) replicate and 2) treatment. The Holm–Sidak multiple comparison procedure (Glantz 2005) in SigmaStat was used to compare means for each species exhibiting a significant treatment effect ($\alpha = 0.05$). The Holm–Sidak multiple comparison procedure controls the experiment-wise error rate at 0.05. For Experiment 1, we also used a 2 by 2 contingency table and the log likelihood ratio (*G*-test) (Zar 1999) to determine if the proportion of traps that detected a given species differed between traps with and without an ethanol lure.

Results

Cerambycidae. We captured a total of 9,526 long-horn beetles in Georgia over the 3-yr period, representing 58 species of Cerambycidae in six subfamilies, and one species of Disteniidae (Table 2). Species in the subfamily Cerambycinae dominated our results, accounting for 98.2% of total catches of beetles and 50.8% of total species. Species diversity and abundance were higher in Experiment 2 (conducted in a pine stand during the spring and early summer) than in Experiments 1 and 3 (conducted in hardwood stands during the summer and fall). The most common genera in trap catches were *Anelaphus*, *Eudercus*, and *Neoclytus*, accounting for 12.8, 19.3, and 57.3% of catches, respectively.

In Experiment 1, traps baited with racemic 3-hydroxyhexan-2-one were attractive to *N. mucronatus* and *N. scutellaris*; attraction was synergized by the addition of ethanol (Fig 1A and B). Similarly, *N. acuminatus* and *N. j. jouteli* Davis were attracted to traps baited with *syn*-2,3-hexanediol with ethanol synergizing attraction (Fig. 1C and D). Attraction of *X. colonus* and *E. quadrigeminata* (Say) to traps baited with racemic 3-hydroxyhexan-2-one was also synergized by the addition of ethanol (Fig. 1E and F). Catches of both species were greater in traps baited with both ethanol and 3-hydroxyhexan-2-one than in traps baited with either compound alone. According to ANOVA, mean catches of *C. dentatus* were unaffected by lure treatments (Fig. 1G) ($F_{5,35} = 1.861$, $P = 0.126$). In terms of detection efficacy, the presence of an ethanol lure significantly increased the proportion of traps that detected *N. scutellaris*, *N. acuminatus*, *E. quadrigeminata*, *Elaphidion mucronatum* Say, *X. colonus*, and *C. dentatus* in Experiment 1 (Table 3).

Table 2. Total numbers of longhorn beetles (Cerambycidae and Disteniidae) captured in three experiments in Georgia (2011–2013)

Family, subfamily, species	Exp 1	Exp 2	Exp 3	Total
Cerambycidae: Parandrinae				
<i>Neandra brunnea</i> (F.)	18	–	1	19
Cerambycidae: Prioninae				
<i>Malodon dasystomus</i> (Say)	–	0	5	5
<i>Orthosoma brunneum</i> (Forster)	5	1	6	12
<i>Prionus imbricornis</i> (L.)	–	–	3	3
<i>Prionus pocularis</i> Dalman	4	–	10	14
Cerambycidae: Spondylidinae				
<i>Asemum striatum</i> (L.)	–	3	–	3
Cerambycidae: Lepturinae				
<i>Bellamira scalaris</i> (Say)	–	3	–	3
<i>Brachyleptura circumdata</i> (Olivier)	–	2	–	2
<i>Centrodera decolorata</i> (Harris)	–	1	–	1
<i>Gaurotes cyanipennis</i> (Say)	–	2	–	2
<i>Gaurotes thoracica</i> (Haldeman)	–	1	–	1
<i>Rhagium inquisitor</i> (L.)	–	20	–	20
<i>Strangalia luteicornis</i> (F.)	–	1	–	1
<i>Typocerus lunulatus</i> (Swederus)	–	1	–	1
<i>Typocerus zebra</i> (Olivier)	–	30	–	30
Cerambycidae: Cerambycinae				
<i>Ancylocera bicolor</i> (Olivier)	–	6	–	6
<i>Anelaphus parallelus</i> (Newman)	–	127	–	127
<i>Anelaphus pumilus</i> (Newman)	–	1,047	–	1,047
<i>Anelaphus villosus</i> (F.)	–	50	1	51
<i>Clytus marginicollis</i> Castelnau & Gory	–	80	–	80
<i>Curius dentatus</i> Newman	36	2	50	88
<i>Cyrtophorus verrucosus</i> (Olivier)	–	96	–	96
<i>Eburia quadrigeminata</i> (Say)	26	–	5	31
<i>Elythridion mucronatum</i> (Say)	11	4	5	20
<i>Elythropterus floridanus</i> (LeConte)	–	3	1	4
<i>Enaphalodes atomarius</i> (Drury)	12	–	1	13
<i>Euderes pini</i> (Olivier)	–	1,837	1	1,838
<i>Heterachthes quadrimaculatus</i> Haldeman	–	–	1	1
<i>Knulliana cincta</i> (Drury)	–	164	–	164
<i>Megaclypeus caryae</i> (Gahan)	–	52	–	52
<i>Molorchus bimaculatus</i> Say	–	45	–	45
<i>Neoclytus acuminatus</i> (F.)	1,623	1,040	362	3,025
<i>Neoclytus caprea</i> (Say)	–	1	–	1
<i>Neoclytus jouteli jouteli</i> Davis	57	–	3	60
<i>Neoclytus mucronatus</i> (F.)	891	153	358	1,402
<i>Neoclytus scutellaris</i> (Olivier)	862	9	92	963
<i>Obrivium maculatum</i> (Olivier)	1	4	–	5
<i>Parelythridion asperatum</i> (Haldeman)	8	0	4	12
<i>Phymatodes amoenus</i> (Say)	–	2	–	2
<i>Phymatodes varius</i> (F.)	–	18	–	18
<i>Stenospheenus notatus</i> (Olivier)	–	11	–	11
<i>Tessaropa tenuipes</i> (Haldeman)	–	1	–	1
<i>Tilloclytus germinatus</i> (Haldeman)	–	4	–	4
<i>Xylotrechus colonus</i> (F.)	74	92	20	186
<i>Xylotrechus sagittatus</i> (Germar)	1	1	–	2
Cerambycidae: Lamiinae				
<i>Acanthocinus nodosus</i> (F.)	–	1	–	1
<i>Aegomorphus modestus</i> (Gyllenhal)	–	1	–	1
<i>Astylopsis macula</i> (Say)	–	–	1	1
<i>Ataxia</i> spp.	–	16	–	16
<i>Ecyrus dasycerus</i> (Say)	–	1	1	2
<i>Eupogonius tomentosus</i> (Haldeman)	–	2	–	2
<i>Graphisurus fasciatus</i> (Degeer)	1	1	–	2
<i>Hyperplatys maculata</i> Haldeman	1	–	–	1
<i>Leptostylus asperatus</i> (Haldeman)	3	2	2	7
<i>Monochamus carolinensis</i> (Olivier)	–	–	2	2
<i>Monochamus titillator</i> (F.)	–	6	–	6
<i>Psenocerus supernotatus</i> (Say)	–	9	–	9
<i>Styloleptus biustus</i> (LeConte)	1	–	–	1
Disteniidae				
<i>Elythrimatatrix undata</i> (F.)	3	–	–	3
Total number of beetles	3,638	4,953	935	9,526
Total number of species	20	47	24	59

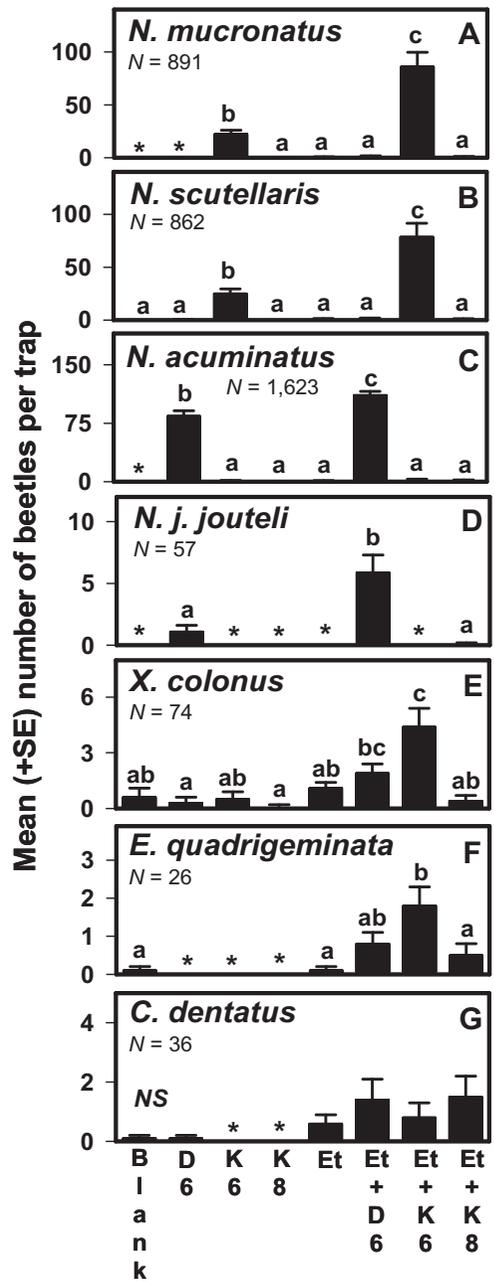


Fig. 1. Experiment 1 – Mean (+ SE) number of: (A) *Neoclytus mucronatus*, (B) *N. scutellaris*, (C) *N. acuminatus*, (D) *N. j. jouteli*, (E) *Xylotrechus colonus*, (F) *Eburia quadrigeminata*, and (G) *Curius dentatus* (Cerambycidae: Cerambycinae) captured in multiple-funnel traps baited with: (Blank) nothing, (D6) *syn*-2,3-hexanediol, (K6) racemic 3-hydroxyhexan-2-one, (K8) racemic 3-hydroxyoctan-2-one, (Et) ethanol, (Et + D6) ethanol and *syn*-2,3-hexanediol, (Et + K6) ethanol and racemic 3-hydroxyhexan-2-one, and (Et + K8) ethanol and racemic 3-hydroxyoctan-2-one. For each species, means followed by the same letter are not significantly different at $P=0.05$ (Holm–Sidak multiple-comparison test). Treatments with an asterisk had zero catches. N =Total trap catch of beetles per location, $NS=P>0.05$.

In Experiment 2, preference for traps baited with ethanol and 3-hydroxyhexan-2-one was demonstrated by *A. pumilus*, *E. pini*, *Knulliana cincta* (Drury), *N. mucronatus*, and *X. colonus* (Fig. 2A–E). In contrast, catches of *Molorchus bimaculatus* Say in ethanol-baited traps were reduced by the addition of 3-hydroxyhexan-2-one (Fig. 2F). Catches of *Anelaphus parallelus*

Table 3. Effect of ethanol lures on the proportion of traps that detected the presence of various beetle species in north-central Georgia, 2011 (Experiment 1)

Family, species	% of traps positive		G^a	P
	Ethanol	No ethanol		
Cerambycidae				
<i>Curius dentatus</i>	50	6	16.7	<0.001
<i>Eburia quadrigeminata</i>	47	3	18.8	<0.001
<i>Enaphalodes atomarius</i>	25	9	2.8	0.090
<i>Elaphidion mucronatum</i>	25	0	12.2	<0.001
<i>Neoclytus acuminatus</i>	91	44	17.2	<0.001
<i>Neoclytus j. jouteli</i>	28	13	2.5	0.116
<i>Neoclytus mucronatus</i>	53	31	3.2	0.075
<i>Neoclytus scutellaris</i>	69	34	7.7	0.005
<i>Xylotrechus colonus</i>	69	19	17.1	<0.001
Bostrichidae				
<i>Xylobiops basilaris</i>	97	44	25.1	<0.001
Cleridae				
<i>Chariessa pilosa</i>	31	25	0.3	0.578
Trogossitidae				
<i>Temnoscheila virescens</i>	69	38	6.4	0.012

There were a total of 64 traps, 32 traps with an ethanol lure, and 32 traps without. Each group had equal numbers of traps baited with *syn*-2,3-hexanediol, racemic 3-hydroxyhexan-2-one, and racemic 3-hydroxyoctan-2-one.

^a Log likelihood ratio for 2 by 2 contingency table.

(Newman) were greater in traps baited with ethanol and *syn*-2,3-hexanediol or ethanol and 3-hydroxyoctan-2-one than in traps baited solely with ethanol; catches in traps baited with ethanol and 3-hydroxyhexan-2-one were intermediary (Fig. 2G). Traps baited with ethanol and *syn*-2,3-hexanediol were preferred by *Anelaphus villosus* (F.), *N. acuminatus*, and *M. caryae* (Fig. 2H–J), whereas *Clytus marginicollis* Castelnau & Gory preferred traps baited with ethanol and 3-hydroxyoctan-2-one (Fig. 2K). The mean (\pm SE) trap catches of *C. verucosus* and *Typocerus zebra* (Olivier) in Experiment 2 were 2.4 ± 0.3 and 0.8 ± 0.1 , respectively, with no treatment effect for either species ($F_{3,27} = 0.769$, $P = 0.521$ and $F_{3,27} = 1.118$, $P = 0.359$, respectively).

Results of Experiment 3 confirmed those of Experiments 1 and 2. The combination of ethanol and 3-hydroxyoctan-2-one was significantly attractive to *N. mucronatus* and *N. scutellaris* (Fig. 3A and B), the combination of ethanol and *syn*-2,3-hexanediol was attractive to *N. acuminatus* (Fig. 3C), and lure treatment had no effect on catches of *C. dentatus* (Fig. 3D) ($F_{3,27} = 1.670$, $P = 0.197$).

Non-Cerambycidae. We captured significant numbers ($N > 25$) of five ambrosia beetle species in Experiments 2–3, with catches of the following species unaffected by trap treatments: *Cnestus mutilatus* (Blandford), *Xyleborinus saxesenii* (Ratzeburg), *Xyleborus* spp., and *Xylosandrus crassiusculus* (Motschulsky) (Table 4). Catches of *Dryoxylon onoharaensum* (Murayama) in ethanol-baited traps were depressed by *syn*-2,3-hexanediol or 3-hydroxyoctan-2-one in Experiment 2 (Table 4). In Experiment 3, catches of *D. onoharaensum* in ethanol-baited traps were depressed by 3-hydroxyoctan-2-one. A bark beetle, *Hypothenemus rotundicollis* Wood & Bright (Curculionidae: Scolytinae), preferred traps baited with ethanol and 3-hydroxyoctan-2-one over those baited with ethanol alone in

Experiments 2–3, and traps baited with ethanol and *syn*-2,3-hexanediol in Experiment 2 (Table 4). Catches of the weevils *Hylobius pales* Herbst and *Stenoscelis brevis* Boheman (Curculionidae) in Experiment 2 were unaffected by treatments ($F_{3,27} = 0.758$, $P = 0.528$ and $F_{3,27} = 0.593$, $P = 0.625$, respectively), with mean (\pm SE) catches of 1.5 ± 0.2 and 2.8 ± 0.3 beetles per trap, respectively.

Xylobiops basilaris (Say) (Bostrichidae) was attracted to traps baited with *syn*-2,3-hexanediol in Experiment 1 with attraction synergized by the addition of ethanol (Fig. 4A). Traps baited with both ethanol and *syn*-2,3-hexanediol were the preferred treatment for *X. basilaris* in Experiments 2–3 as well (Figs. 5A and 6A). In all three experiments, catches of *X. basilaris* in traps baited with the combination of ethanol and 3-hydroxyhexan-2-one were greater than those in ethanol-baited traps but less than those in traps baited with both ethanol and *syn*-2,3-hexanediol. Trap treatments had no effect on catches of *Buprestis lineata* F. (Buprestidae) in Experiment 2 ($F_{3,27} = 2.442$, $P = 0.086$), with a mean (\pm SE) catch of 4.0 ± 0.5 beetles per trap.

3,2-Hydroxyketones and *syn*-2,3-hexanediol affected catches of several beetle predators. In Experiment 1, 3-hydroxyhexan-2-one was attractive to *Temnoscheila virescens* (F.) (Trogossitidae), with ethanol synergizing the response (Fig. 4B). Similarly, in Experiments 2–3, traps baited with ethanol and 3-hydroxyhexan-2-one were preferred by *T. virescens* (Figs. 5B and 6B). In Experiment 1, catches of *Tenebroides* spp. (Trogossitidae) were affected by lure treatments ($F_{7,49} = 0.136$, $P = 0.008$), although the Holm–Sidak test was unable to find differences between treatment means (Fig. 4C). In Experiment 2, catches of *Tenebroides* spp. in traps baited with ethanol and 3-hydroxyhexan-2-one were less than those baited with ethanol and 3-hydroxyoctan-2-one (Fig. 5C), whereas there was no treatment effect in Experiment 3 (Fig. 6C) ($F_{3,27} = 1.097$, $P = 0.3688$).

Chariessa pilosa (Forster) (Cleridae) was attracted to traps baited with ethanol and *syn*-2,3-hexanediol in Experiments 1–2 (Figs. 4D and 5D), whereas the larval ectoparasite *Catogenus rufus* F. (Passandridae) was unaffected by trap treatments ($F_{3,27}$, $P = 0.303$) in Experiment 2 (Fig. 5E). In Experiment 2, the bee assassin bug, *Apiomerus crassipes* (F.) (Hemiptera: Reduviidae), showed a strong response to traps baited with ethanol and 3,2-hydroxyketones, particularly 3-hydroxyhexan-2-one (Fig. 5F).

Discussion

The goal of our study was fully realized by demonstrating attraction of 13 species of cerambycids in north-central Georgia to traps baited with ethanol and one of the following pheromones: 1) racemic 3-hydroxyhexan-2-one; 2) racemic 3-hydroxyoctan-2-one; and 3) *syn*-2,3-hexanediol (Figs. 1–3). Traps baited with ethanol and racemic 3-hydroxyhexan-2-one were attractive to the following seven species: *A. pumilus*, *E. quadrigeminata*, *E. pini*, *K. cincta*, *N. mucronatus*, *N. scutellaris*, and *X. colonus*. Traps baited with both ethanol and *syn*-2,3-hexanediol were attractive to the following four

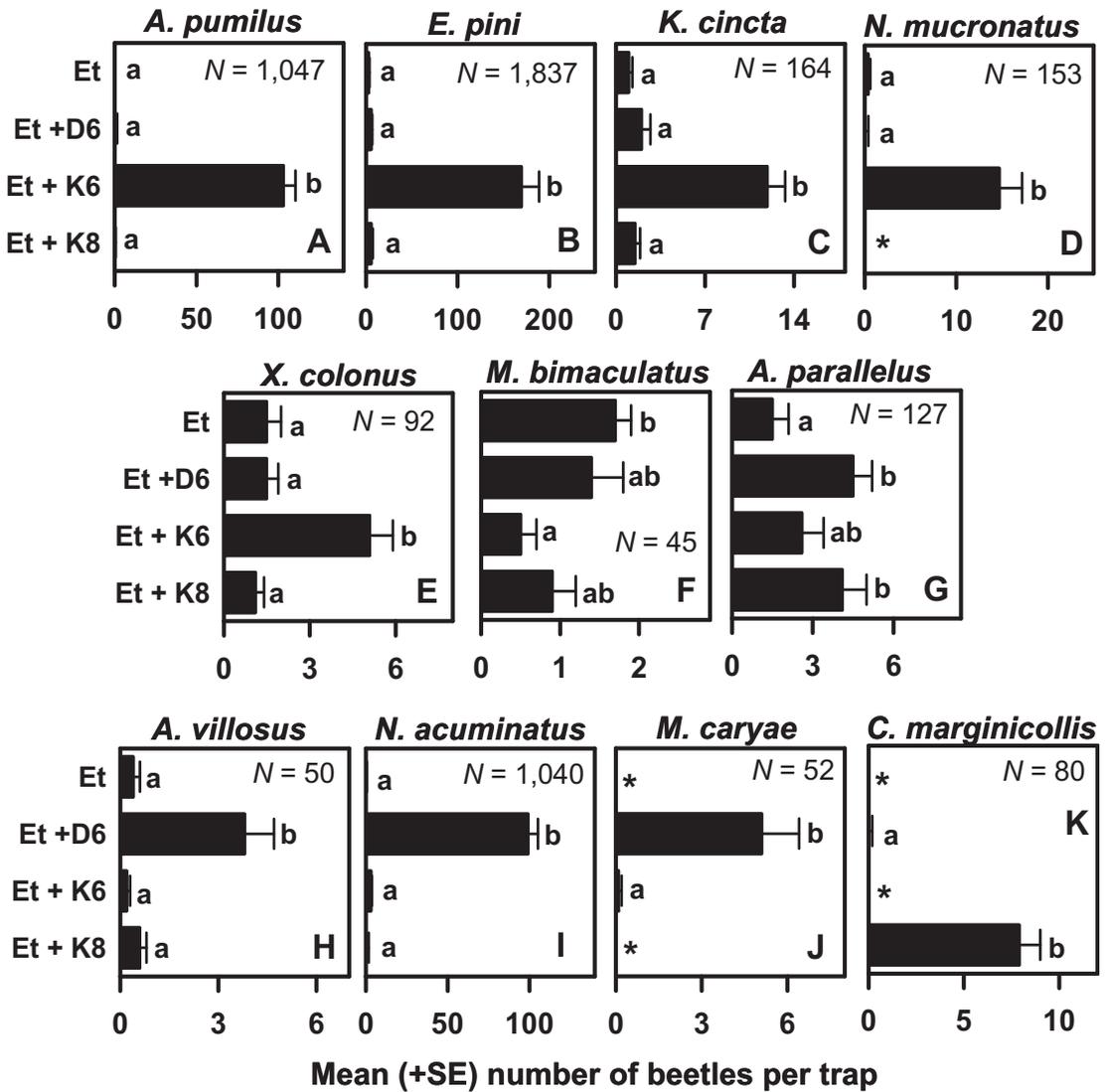


Fig. 2. Experiment 2 – Mean (+SE) number of: *Anelaphus pumilus* (A), *Euderces pini* (B), *Knulliana cincta* (C), *Neoclytus mucronatus* (D), *Xylotrechus colonus* (E), *Molorchus bimaculatus* (F), *A. parallelus* (G), *A. villosus* (H), *N. acuminatus* (I), *Megaclyllene caryae* (J), and *Clytus marginicollis* (K) (Cerambycidae: Cerambycinae) captured in multiple-funnel traps baited with ethanol (Et), ethanol and *syn*-2,3-hexanediol (Et + D6), ethanol and racemic 3-hydroxyhexan-2-one (Et + K6), and ethanol and racemic 3-hydroxyoctan-2-one (Et + K8). For each species, means followed by the same letter are not significantly different at $P=0.05$ (Holm–Sidak multiple-comparison test). Treatments with an asterisk had zero catches. N = Total trap catch of beetles per location, $NS = P > 0.05$.

species: *A. villosus*, *M. caryae*, *N. acuminatus*, and *N. j. jouteli*. *Anelaphus parallelus* was attracted to traps baited either with ethanol and *syn*-2,3-hexanediol or ethanol and racemic 3-hydroxyoctan-2-one (Fig. 2G). Only *C. marginicollis* exhibited a clear preference for traps baited with ethanol and racemic 3-hydroxyoctan-2-one over all other treatments (Fig. 2H).

To the best of our knowledge, attraction to traps baited with *syn*-2,3-hexanediol or 3,2-hydroxyketones has not been previously reported for *C. marginicollis*, *E. quadrigeminata*, and *N. j. jouteli*. Our data provide additional support for the hypothesis that the

hydroxyketone/hexanediols structural motif is highly conserved within the Cerambycinae (Allison et al. 2004, Ray et al. 2006, Hanks et al. 2007, Hanks and Millar 2013, Ray et al. 2015). Additionally, 3,2-hydroxyketones and 2,3-hexanediols have been identified as pheromones of cerambycine species in Europe and Asia (Schröder et al. 1994, Leal et al. 1995), increasing detection efficacy in traps in those regions (Nakamura 1994, Sweeney et al. 2014).

We found no evidence of geographic variation in responses of cerambycids to *syn*-2,3-hexanediol and 3,2-hydroxyketones. Our results for *A. pumilus*, *A.*

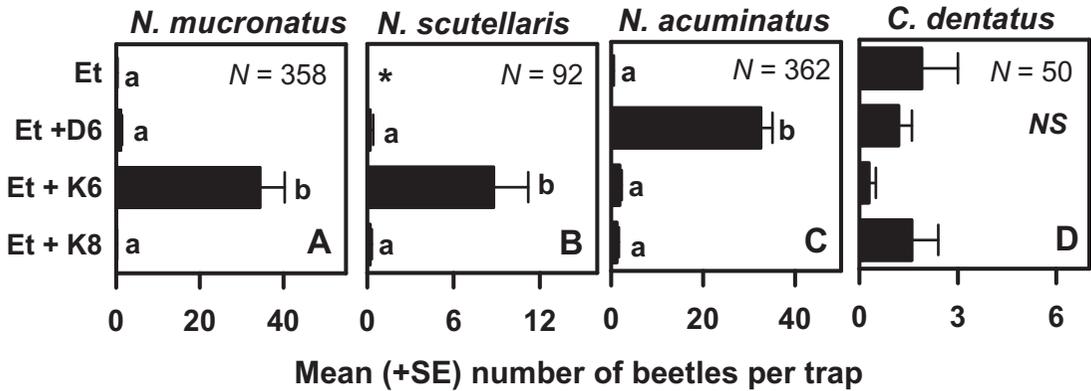


Fig. 3. Experiment 3 – Mean (+ SE) number of *Neoclytus mucronatus* (A), *N. scutellaris* (B), *N. acuminatus* (C), and *Curius dentatus* (D) (Cerambycidae: Cerambycinae) captured in multiple-funnel traps baited with ethanol (Et), ethanol and syn-2,3-hexanediol (Et + D6), ethanol and racemic 3-hydroxyhexan-2-one (Et + K6) and ethanol and racemic 3-hydroxyoctan-2-one (Et + K8). For each species, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak multiple-comparison test). N = Total trap catch of beetles per location, $NS = P > 0.05$.

Table 4. Catches of bark and ambrosia beetles (Curculionidae: Scolytinae) in traps baited with ethanol (Et), ethanol and 2,3-hexanediol (Et + D6), ethanol and 3-hydroxyhexan-2-one (Et + K6), and ethanol and 3-hydroxyoctan-2-one (Et + K8) in Exp 2–3

Species	N	Mean (\pm SE) number of beetles per trap				ANOVA	
		Et	Et + D6	Et + K6	Et + K8	$F_{(3,27)}$	P
Exp 2							
<i>Cnestus mutillatus</i>	518	12.3 \pm 2.2	14.7 \pm 2.4	9.4 \pm 1.7	15.4 \pm 2.3	2.050	0.131
<i>Dryoxylon onoharaensum</i>	113	3.9 \pm 0.8b	1.9 \pm 0.5a	3.9 \pm 0.6b	1.6 \pm 0.4a	4.175	0.015
<i>Hypothenemus rotundicollis</i>	181	1.6 \pm 0.4a	4.9 \pm 1.5b	2.1 \pm 0.4ab	9.5 \pm 1.7c	11.526	<0.001
<i>Xyleborinus saxesenii</i>	260	7.8 \pm 1.2	4.6 \pm 0.5	6.9 \pm 1.1	7.7 \pm 1.2	2.109	0.123
<i>Xyleborus</i> spp.	69	1.9 \pm 0.3	1.3 \pm 0.3	2.5 \pm 0.6	1.2 \pm 0.4	1.967	0.143
<i>Xylosandrus crassiusculus</i>	54	1.4 \pm 0.4	0.6 \pm 0.3	1.4 \pm 0.4	1.8 \pm 0.5	1.784	0.174
Exp 3							
<i>Dryoxylon onoharaensum</i>	713	25.6 \pm 3.0b	21.3 \pm 2.2b	18.2 \pm 2.8b	6.2 \pm 1.0a	21.740	<0.001
<i>Hypothenemus rotundicollis</i>	733	4.8 \pm 1.1a	5.1 \pm 0.9a	6.3 \pm 1.4a	57.7 \pm 11.4b	64.859	<0.001
<i>Xyleborinus saxesenii</i>	92	2.2 \pm 0.4ab	2.5 \pm 0.6ab	3.5 \pm 0.6b	1.0 \pm 0.4a	5.030	0.007
<i>Xyleborus</i> spp.	37	0.6 \pm 0.2	1.4 \pm 0.4	1.0 \pm 0.5	0.7 \pm 0.4	1.334	0.284
<i>Xylosandrus crassiusculus</i>	41	0.7 \pm 0.3	1.0 \pm 0.4	2.0 \pm 0.7	0.4 \pm 0.2	2.512	0.080

N, total number of beetles captured.

parallelus, *A. villosus*, *E. pini*, *M. caryae*, *N. acuminatus*, *N. mucronatus*, *N. scutellaris*, and *X. colonus* in Georgia are fully consistent with those of Lacey et al. (2004, 2007, 2008, 2009), Wong et al. (2012), Ray et al. (2015), and Mitchell et al. (2015) in Illinois; Mitchell et al. (2013) in Michigan; and Hanks and Millar (2013) in Pennsylvania. The lack of attraction of *C. dentatus* to syn-2,3-hexanediol in our study in Georgia agrees with Lacey et al. (2004), who found that *C. dentatus* in Illinois was attracted to a blend of all four stereoisomers of 2,3-hexanediols but not to a 50:50 mix of (2*R*,3*R*)- and (2*S*,3*S*)-hexanediols, suggesting that the pheromone of this species may contain either (2*R*,3*S*)-hexanediol or (2*S*, 3*R*)-hexanediol. Our results provide evidence that managers responsible for surveillance of exotic longhorn beetles in Europe and Asia do not need to be concerned about using geographic-specific lures.

We found no evidence that ethanol interrupted attraction of any species of Cerambycidae in our study. In answer to our first objective, we found that ethanol synergized the responses of six cerambycine species to

traps baited with syn-2,3-hexanediol or 3-hydroxyhexan-2-one in Experiment 1 (Fig. 1A–F). The addition of an ethanol lure to traps baited with hexanediols and hydroxyhexanones increased mean catches significantly, whereas mean catches in traps baited with ethanol alone did not differ from those in unbaited traps. In fact, the responses of three species (*N. j. jouteli*, *X. colonus*, and *E. quadrigeminata*) would likely not have been detected without the addition of ethanol. The presence of an ethanol lure increased the efficacy of detecting cerambycine species in traps, including *C. dentatus*. Depending on the species of longhorn beetle, 25–91% of traps with ethanol lures detected their presence at the Oconee National Forest site in 2011, compared with only 0–44% of traps without ethanol lures (Table 3). Our results should help to alleviate any concern about the use of ethanol as a diluent in the manufacture of 2,3-hexanediol and 3,2-hydroxyketone lures as well as encourage the addition of an ethanol lure to traps baited with 2,3-hexanediol and hydroxyketone lures.

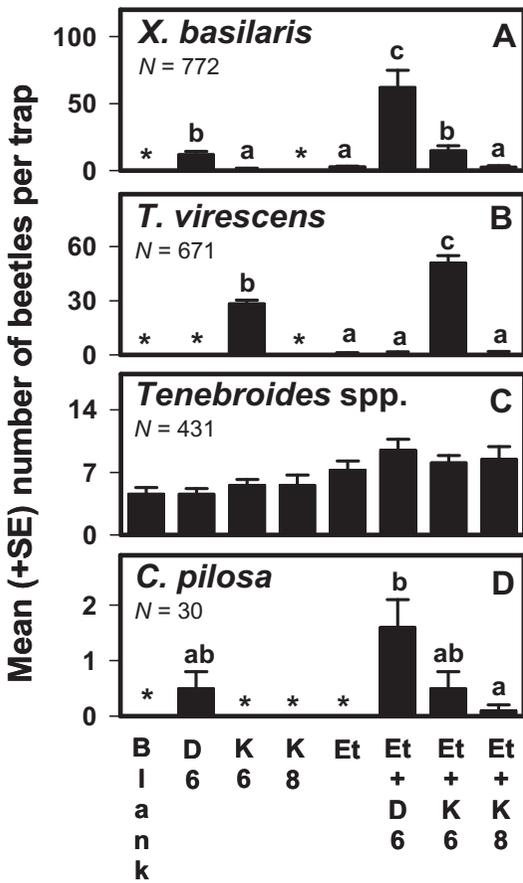


Fig. 4. Experiment 1 – Mean (+ SE) number of *Xylobiops basilaris* (A) (Bostrichidae), *Temnoscheila virescens* (B), *Tenebroides* spp. (C) (Trogossitidae), and *Chariessa pilosa* (D) (Cleridae) captured in multiple-funnel traps baited with nothing (Blank), *syn*-2,3-hexanediol (D6), racemic 3-hydroxyhexan-2-one (K6), racemic 3-hydroxyoctan-2-one (K8), ethanol (Et), ethanol and *syn*-2,3-hexanediol (Et + D6), ethanol and racemic 3-hydroxyhexan-2-one (Et + K6), and ethanol and racemic 3-hydroxyoctan-2-one (Et + K8). For each species, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak multiple-comparison test). Treatments with an asterisk had zero catches. N = Total trap catch of beetles per location.

In answer to our second objective, we found that catches of four of five common species of adventive xyloborine ambrosia beetles in ethanol-baited traps were largely unaffected by the presence of *syn*-2,3-hexanediol or 3,2-hydroxyketones (Table 4). The addition of racemic 3-hydroxyoctan-2-one to ethanol-baited traps did reduce catches of *D. onoharaensum* and increased catches of the bark beetle, *H. rotundicollis*. Similarly, *syn*-2,3-hexanediol reduced catches of *D. onoharaensum* and increased catches of *H. rotundicollis* (in Experiment 2 but not Experiment 3) and the bostrichid beetle, *X. basilaris* (Figs. 4A, 5A, and 6A). Noseworthy et al. (2012) reported increases in catch of the ambrosia beetle, *Monarthrum scutellare* (LeConte), when racemic 3-hydroxyoctan-2-one was added to

ethanol-baited traps. Our results and those of Noseworthy (2012) suggest that adding cerambycine pheromones to traps baited with ethanol would not significantly reduce the efficacy of detecting Scolytinae species in trapping surveillance programs and would be less costly than deploying longhorn beetle pheromones and ethanol in separate traps.

The attraction of some bark and ambrosia beetle species to the combination of ethanol and cerambycine pheromones suggests these species may use these compounds as kairomones to assist in locating suitable hosts for oviposition. Many longhorn species infest stressed and moribund hosts (Linsley 1961, Solomon 1995, Hanks 1999) like those colonized by many species of bark and ambrosia beetles (Furniss and Carolin 1980, USDA 1985). Bark beetle pheromones are used as kairomones by some ambrosia beetles such as *Gnathotrichus materiarius* (Fitch) (Miller et al. 2011) and some longhorn beetle species (Allison et al. 2004, Pajares et al. 2004). Negative responses to racemic 3-hydroxyoctan-2-one by the ambrosia beetle *D. onoharaensum* suggest that the pheromone may indicate an unsuitable host, e.g., one at risk of prior or pending colonization by potential competitors. *D. onoharaensum* is an adventive species that is widely distributed in the United States (Bright and Rabaglia 1999, Lightle et al. 2007). Little is published on the biology of *D. onoharaensum*, but it has been recorded infesting the stems of live *Populus deltoides* Bartram ex Marshall in South Carolina (Coyle et al. 2005).

Several species of common bark beetle predators were attracted to baited traps in our study. Species such as *T. virescens* (Trogossitidae) and *C. pilosa* (Cleridae) prey on adult bark beetles as adults, and on bark beetle larvae as larvae (USDA 1985). Whether or not these species prey on Cerambycinae is unclear. However, *T. virescens* was consistently attracted to traps baited with 3-hydroxyhexan-2-one, with or without ethanol (Figs. 4B, 5B, and 6B), whereas *C. pilosa* was attracted to traps baited with ethanol and *syn*-2,3-hexanediol (Figs. 4D and 5D). These results suggest these species may have the opportunity to prey on some cerambycine species (larval or adult) by responding to these compounds as kairomones. The beetle predator, *Tenebroides* spp., and the ectoparasite, *C. rufus*, were largely unaffected by trap treatments (Figs. 4C, 5E, and 6C).

One of several surprising results in our study was the attraction of the bee assassin bug, *A. crassipes*, to traps baited with ethanol and 3,2-hydroxyketones. Species in this genus commonly prey on bees and other insects that feed on flowers. A number of Cerambycinae species feed and aggregate on flowers (Linsley 1961). Floral volatiles synergize attraction of *Anaglyptus subfasciatus* Thomson (Cerambycinae) to its hydroxyketone pheromones (Nakamura et al. 1997). It is possible that 3,2-hydroxyketones act as kairomones for assassin bugs as well as other predators.

There is a great deal to unravel about the roles of alkanediols and hydroxyketones in the chemical ecology of forest insects. One critical issue is the source of these pheromones. They are likely emitted from

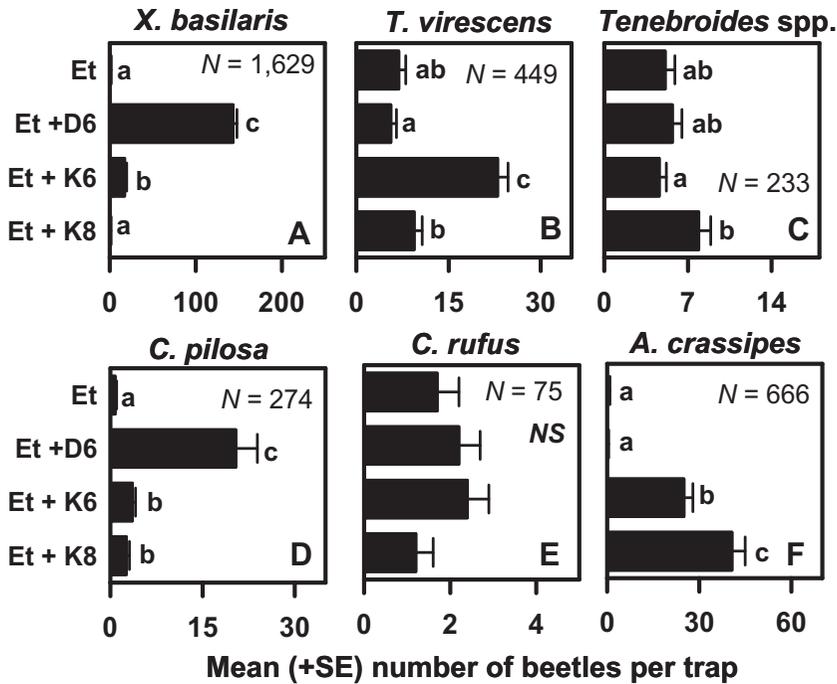


Fig. 5. Experiment 2 – Mean (+ SE) number of *Xylobiops basilaris* (A) (Bostrichidae), *Temnoscheila virescens* (B), *Tenebroides* spp. (Trogossitidae), (C), *Charriessa pilosa* (D) (Cleridae), *Catogenus rufus* (E) (Passandridae), and *Apiomerus crassipes* (F) (Hemiptera: Reduviidae), captured in multiple-funnel traps baited with ethanol (Et), ethanol and *syn*-2,3-hexanediol (Et + D6), ethanol and racemic 3-hydroxyhexan-2-one (Et + K6), and ethanol and racemic 3-hydroxyoctan-2-one (Et + K8). For each species, means followed by the same letter are not significantly different at $P=0.05$ (Holm–Sidak multiple-comparison test). N = Total trap catch of beetles per location, $NS = P > 0.05$.

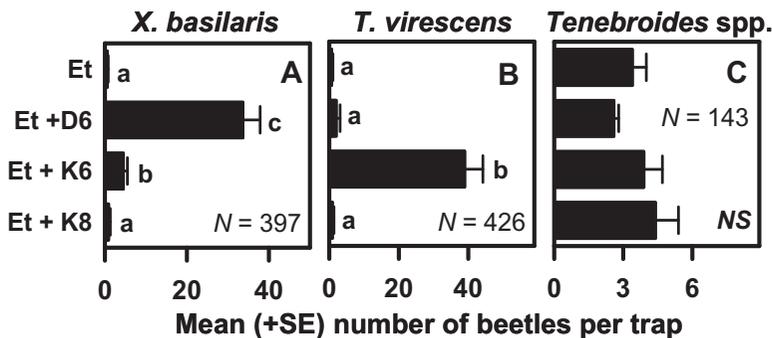


Fig. 6. Experiment 3 – Mean (+ SE) number of *Xylobiops basilaris* (A) (Bostrichidae), *Temnoscheila virescens* (B), and *Tenebroides* spp. (C) (Trogossitidae), and captured in multiple-funnel traps baited with ethanol (Et), ethanol and *syn*-2,3-hexanediol (Et + D6), ethanol and racemic 3-hydroxyhexan-2-one (Et + K6), and ethanol and racemic 3-hydroxyoctan-2-one (Et + K8). For each species, means followed by the same letter are not significantly different at $P=0.05$ (Holm–Sidak multiple-comparison test). N = Total trap catch of beetles per location, $NS = P > 0.05$.

prothoracic gland pores in males (Ray et al. 2006). But where and how are they manufactured? Are pheromone precursors ingested as larvae or as adults? Are they derived from flowers, catkins, or woody material? Flowers typically have complex bouquets designed to attract a broad array of insect species. Do these compounds serve as aggregation pheromones for species of Cerambycinae as well as kairomones for other species? Understanding such issues may provide information to

managers of detection programs concerning optimal locations for traps as well as to chemical ecologists concerning evolutionary history and current selection pressures.

The challenge in designing surveillance programs is to develop an optimal combination of traps and different lure blends that maximizes the efficacy of detecting the species of longhorn beetles present at a given site, within budget limits. Our results provide support for

lures that can increase trap catch and diversity. We still need to determine the effects of combining alkanediols and hydroxyketones in the same traps. Moreover, though we can measure the relative efficacy of different lures for detecting a given species, we do not know the relationship between mean catch and population density for any lure or for any longhorn beetle species, because population levels are unknown. Our goal is to find a measure of efficacy that truly reflects our ability to detect rare species when first introduced into new habitats.

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