*Journal of Economic Entomology*, 111(1), 2018, 252–259
doi: 10.1093/jee/tox312
Advance Access Publication Date: 8 December 2017
Research Article



# Identifying Possible Pheromones of Cerambycid Beetles by Field Testing Known Pheromone Components in Four Widely Separated Regions of the United States

**Jocelyn G. Millar,[1] Robert F. Mitchell,[2,3] Judith A. Mongold-Diers,[2] Yunfan Zou,[1] Carlos E. Bográn,[4] Melissa K. Fierke,[5] Matthew D. Ginzel,[6] Crawford W. Johnson,[7] James R. Meeker,[7] Therese M. Poland,[8] Iral Ragenovich,[9] and Lawrence M. Hanks[2,10]**

[1]Department of Entomology, University of California, Riverside, CA 92521, [2]Department of Entomology, University of Illinois at Urbana-Champaign, Urbana, IL 61801, [3]Current address: Department of Biology, University of Wisconsin Oshkosh, Oshkosh, WI 54901, [4]OHP Inc., College Station, TX 77845, [5]Department of Environmental and Forest Biology, State University of New York, Syracuse, NY 13210, [6]Department of Entomology, Purdue University, West Lafayette, IN 47907-2089, [7]USDA Forest Service, Southern Region, Pineville, LA 71360, [8]USDA Forest Service, Northern Research Station, Lansing, MI 48910, [9]USDA Forest Service, Pacific Northwest Region, Portland, OR 97204, and [10]Corresponding author, e-mail: hanks@life.illinois.edu

Subject Editor: Timothy Schowalter

Received 14 September 2017; Editorial decision 16 October 2017

## Abstract

The pheromone components of many cerambycid beetles appear to be broadly shared among related species, including species native to different regions of the world. This apparent conservation of pheromone structures within the family suggests that field trials of common pheromone components could be used as a means of attracting multiple species, which then could be targeted for full identification of their pheromones. Here, we describe the results of such field trials that were conducted in nine states in the northeastern, midwestern, southern, and western United States. Traps captured 12,742 cerambycid beetles of 153 species and subspecies. Species attracted in significant numbers to a particular treatment (some in multiple regions) included 19 species in the subfamily Cerambycinae, 15 species in the Lamiinae, one species in the Prioninae, and two species in the Spondylidinae. Pheromones or likely pheromones for many of these species, such as 3-hydroxyhexan-2-one and *syn*- and *anti*-2,3-hexanediols for cerambycine species, and fuscumol and/or fuscumol acetate for lamiine species, had already been identified. New information about attractants (in most cases likely pheromone components) was found for five cerambycine species (*Ancylocera bicolor* [Olivier], *Elaphidion mucronatum* [Say], *Knulliana cincta cincta* [Drury], *Phymatodes aeneus* LeConte, and *Rusticoclytus annosus emotus* [Brown]), and five lamiine species (*Ecyrus dasycerus dasycerus* [Say], *Lepturges symmetricus* [Haldeman], *Sternidius misellus* [LeConte], *Styloleptus biustus biustus* [LeConte], and *Urgleptes signatus* [LeConte]). Consistent attraction of some species to the same compounds in independent bioassays demonstrated the utility and reliability of pheromone-based methods for sampling cerambycid populations across broad spatial scales.

**Key words:** chemical ecology, pheromones, monitoring

Research during the last decade has revealed that mate finding in many cerambycid beetle species is mediated by volatile pheromones which may be either produced by males and attract both sexes (i.e., aggregation-sex pheromones, for species in the subfamilies Cerambycinae, Lamiinae, and Spondylidinae), or produced by females and attract only males (sex pheromones, for species in the Lepturinae and Prioninae; reviewed in Millar and Hanks 2017). Some pheromone structures are broadly shared among closely related species (e.g., congeners), or even among more distantly related species in different subfamilies. Furthermore, pheromone compounds may be shared among sympatric species, as well as by species native to different continents which have been separated for millions of years (e.g., species native to North and South America, Eurasia, and Australia). Common components of aggregation-sex pheromones of cerambycines include the 3-hydroxyalkan-2-ones and related 2,3-alkanediols, while those of lamiines include (*E*)-6,10-dimethyl-5,9-undecadien-2-ol (fuscumol), its corresponding acetate (fuscumol acetate), and 2-(undecyloxy) ethanol (monochamol). Analogously, 3,5-dimethyldodecanoic acid (prionic acid) and specific stereoisomers of 2,3-hexanediol serve as female-produced sex pheromones for a number of prionine species

(Hanks and Millar 2016). Conversely, evidence is accumulating that some cerambycid species use pheromones that appear to be shared much more narrowly (e.g., only among congeners), or that may possibly be species specific (Ray et al. 2011; Zou et al. 2015; Silva et al. 2016a,b; Millar et al. 2017).

The apparent conservation of a number of pheromone structures within the Cerambycidae worldwide suggests that field bioassays of common pheromone components could be used as an efficient way to attract multiple species, including species whose pheromones have not yet been identified. These species could then be targeted for full identification of their pheromones. For species in the Cerambycinae, Lamiinae, and Spondylidinae, all of which have male-produced aggregation-sex pheromones which attract both sexes, identifications would be expedited because live trapping with pheromone lures would provide a ready source of both sexes for preparation of pheromone extracts for analysis. The efficacy of this approach has been demonstrated by research in the United States (e.g., Hanks et al. 2007, Mitchell et al. 2013, Meier et al. 2016, Miller et al. 2017) and Asia (Sweeney et al. 2014; Wickham et al. 2014, 2016). Follow-up research to fully identify the pheromones of individual species has shown that attraction of a species to traps baited with a particular chemical or a blend of chemicals is usually a reliable predictor of pheromone chemistry (Millar and Hanks 2017).

Here, we describe results from field testing a number of known cerambycid pheromone components in four widely separated geographic regions of the United States, spanning nine states. Our goals were: 1) to assess the utility of using pheromone-baited traps to sample the taxonomic diversity of cerambycids within and among various regions, and 2) to use the attraction of various species to particular compounds or blends as leads to identifying their pheromones. Thus, pheromone-baited traps were deployed in states of the northeastern (Vermont, New Hampshire, New York), midwestern (Michigan, Indiana), southern (Mississippi, Louisiana, Texas), and western United States (Oregon). We present the complete list of species that were captured as a contribution to the literature on their geographical distributions. We also test for statistically significant levels of attraction that might provide indications as to the likely pheromone chemistry of particular species.

## Materials and Methods

### Sources of Chemicals

Racemic *syn*- and *anti*-2,3-alkanediols, the complete blend of all four diol stereoisomers, and racemic 3-hydroxyoctan-2-one and 3-hydroxydecan-2-one (henceforth ketols) were synthesized as described in Lacey et al. (2004, 2007). For convenience, the chemical names of diols and ketols are abbreviated to specify stereochemistry and carbon chain-length, such as '*syn*-C6-diol' for *syn*-2,3-hexanediol, and C8-ketol for racemic 3-hydroxyoctan-2-one. Other compounds were purchased from commercial sources, including racemic 3-hydroxyhexan-2-one (C6-ketol), racemic fuscumol, racemic fuscumol acetate, and monochamol (all from Bedoukian Research Inc., Danbury, CT), and racemic 2-methylbutan-1-ol (Aldrich Chemical, Milwaukee, WI).

### Study Sites

Collaborators were responsible for identifying suitable sites for bioassays in the nine states, which are listed in Table 1. Study sites were stands of mixed hardwood and/or coniferous trees in natural or managed environments.

### General Methods of Trapping

Beetles were caught with black panel traps (cross-vane, corrugated plastic; AlphaScents, Portland, OR) or 12-unit plastic funnel traps (Contech Enterprises Inc., Victoria, British Columbia, Canada), all of which were coated with Fluon (a fluoropolymer liquid dispersion; Northern Products Inc., Woonsocket, RI) or dry-film Teflon lubricant (a fluoropolymer aerosol; Non-Stick, Dupont, now Chemours, Wilmington, DE) to improve trapping efficiency (Graham et al. 2010). Basins of traps were partly filled with diluted propylene glycol to kill and preserve captured beetles.

Traps were suspended from tree branches (sites in New Hampshire, Vermont), or hung from supports constructed of polyvinyl chloride pipe, aluminum conduit, steel reinforcing bar, or fence posts, at a height of <2 m above ground. Pheromone lures were polyethylene sachets (press-seal bags, Bagette model 14770, 5.1 × 7.6 cm, 0.05 mm wall thickness, Cousin Corp., Largo, FL) that were loaded with 50 mg of the racemic compounds (i.e., 25 mg of each enantiomer), or 25 mg of the achiral monochamol, in 1 ml of solvent (ethanol in 2010, subsequently isopropanol). Control lures contained 1 ml of the appropriate solvent.

Release rates of the various test compounds were estimated by aerating lures using the same method and apparatus that was used in collecting insect-produced compounds (e.g., Meier et al. 2016). Briefly, individual lures were placed upright in glass jars through which purified air was drawn, and volatiles were collected with glass tube cartridges containing a layer of the adsorbent Hayesep Q (150 mg, Sigma-Aldrich, St. Louis, MO). Lures were held for 24 h after loading to allow release rates to stabilize, and then were aerated under ambient laboratory conditions (~20°C). The aeration time necessary to yield measurable quantities of the chemical in question was determined by experimentation and ranged from 1 h for the more volatile compounds (ketols, fuscumol acetate) to 11 d for the much less volatile prionic acid. Chemicals were recovered from adsorbent cartridges by extraction with 1.5 ml of dichloromethane spiked with the internal standard eicosane. Estimated release rates (in mg/d) were as follows: C6-ketol (2.1), C8-ketol (1.5), C10-ketol (0.51), *syn*-C6-diol (0.15), *anti*-C6-diol (0.094), *syn*-C8-diol (0.099), *anti*-C8-diol (0.031), fuscumol (0.15), fuscumol acetate (0.30), monochamol (0.018), prionic acid (0.00069). Release rates of the components from lures loaded with binary blends were similar to those for lures loaded with the individual compounds.

Traps were deployed 5 to 50 m apart in linear transects. Independent field experiments have confirmed that separating traps by at least 5 m within transects minimizes interference among treatments (Wong et al. 2017). Treatments were assigned randomly to traps on the day of set up, with one treatment per transect. The number of transects per state varied from one to four, and pairs of transects were widely separated (Table 1). Transects in Vermont and New Hampshire were replicates of the same study, and therefore data from those states were combined for analysis. Traps were serviced at intervals of 2–14 d, at which time treatments were either rotated down transects, or their positions were re-randomized, to control for positional effects. At the four Texas sites, however, treatments were assigned arbitrarily to traps on the day of set up, but were not moved subsequently.

### Field Experiments

Experimental treatments were intended to test a broad range of known pheromone components of cerambycids, and varied across states. The most common treatments included the cerambycine pheromones C6-ketol and racemic *syn*- and *anti*-C6-diols, and the

**Table 1.** Study sites for field bioassays of synthesized pheromones of cerambycids conducted in various regions of the United States during 2010 and 2013, the nature of the surrounding forests, and experimental treatments

| Location of study sites | GPS (lat., long.) | Forest type | Treatments (timing of experiment) |
|---|---|---|---|
| *Vermont* (Addison Co.) | | | |
| Near Goshen | 43.849, −73.014 | Mixed hardwoods | C6-ketol, *syn*-C6-diol, *anti*-C6-diol, C6-ketol + C6-diol, fuscumol + fuscumol acetate, solvent control (24 May–3 August 2010: 71 d) |
| Near Middlebury | 43.998, −73.158 | | |
| *New Hampshire* (Rockingham Co.) | | | |
| Urban For. Center, Portsmouth | 43.044, −70.769 | Mixed hardwood-conifer | |
| *New York* | | | |
| SUNY-ESF James F. Dubuar Memorial For., Adirondack Park, St. Lawrence Co. | 44.163, −74.908 | Mature hardwoods, managed conifers | C6-ketol, *syn*-C6-diol, *anti*-C6-diol, fuscumol, fuscumol acetate, monochamol, solvent control, blank control (18 May–10 September 2010: 115 d) |
| Frank E. Jadwin State For., Lewis Co. | 44.076, −75.381 | Mature northern hardwoods | |
| SUNY-ESF Lafayette Road Field Station, Onondaga Co. | 42.991, −76.132 | Arboretum: many hardwood and conifer species | |
| SUNY-ESF Heiberg Memorial For., Cortland Co. | 42.768, −76.072 | Mixed hardwoods and managed conifers | |
| Allegany State Park, Cattaraugus Co. | 42.091, −78.851 | Mixed hardwoods and conifers | |
| *Michigan* (Ingham Co.) | | | |
| Michigan State Univ. Tree Res. Center, Lansing | 42.672, −84.475 | Mixed hardwoods | Expt. 1: C6-ketol, C8-ketol, C10-ketol, C6-ketol + C8-ketol, C8-ketol + C10-ketol, solvent control (19 May–13 September 2013: 107 d)<br>Expt. 2: *syn*-C6-diol, *syn*-C8-diol, *syn*-C6- + *syn*-C8-diol, *anti*-C6-diol, *anti*-C8-diol, *anti*-C6-diol + *anti*-C8-diol, solvent control (23 May–13 September 2013: 113 d) |
| *Indiana* (Tippecanoe Co.) | | | |
| Martell Forest (2 transects) | 40.435, −87.034; 40.442, −87.035 | Mixed hardwoods | C6-ketol, C8-ketol, *syn*-C6-diol, *syn*-C8-diol, *anti*-C6-diol, *anti*-C8-diol, fuscumol, fuscumol acetate, monochamol, solvent control (25 May–5 October 2010, 133 d) |
| *Mississippi* | | | |
| USDA Delta Expt. For., Washington Co. (2 transects) | 33.474, −90.902; 33.455, −90.928 | Bottomland mixed hardwoods | C6-ketol, C8-ketol, *syn*-C6-diol, *syn*-C8-diol, *anti*-C6-diol, *anti*-C8-diol, fuscumol, fuscumol acetate, monochamol, solvent control (11 June–2 July 2010, 21 d) |
| Delta Natl. For., Sharkey Co. | 32.849, −90.806 | | |
| *Louisiana* (Grant Parish) | | | |
| Stuart Lake | 31.481, −92.482 | All mixed pine-hardwood sawtimber clear-cuts completed within previous 6 mo | C6-ketol, *syn*-C6-diol, *anti*-C6-diol, C6-ketol + C6-diol, fuscumol + fuscumol acetate, solvent control (3 May–9 July 2010, 47 d) |
| Kisatchie Natl. Forest | 31.701, −92.554 | | |
| Iatt Lake | 31.577, −92.615 | | |
| *Texas* | | | |
| Wellborn, Brazos Co. | 30.478, −96.233 | Commercial nurseries surrounded by hardwood or coniferous forests, agricultural fields, or grasslands | C6-ketol, *syn*-C6-diol, *anti*-C6-diol, fuscumol + fuscumol acetate, monochamol, high release ethanol (17 May–17 September 2010) |
| Hempstead, Waller Co. | 29.997, −96.099 | | |
| Tomball, Harris Co. | 30.098, −95.706 | | |
| Willis, Montgomery Co. | 30.419, −95.543 | | |
| *Oregon* | | | |
| Fish Creek, Clackamas River Ranger Dist., Mt. Hood Natl. For., Clackamas Co. | 45.137, −122.151 | Mixed hardwood-conifer | C6-ketol, *syn*-C6-diol, *anti*-C6-diol, C6-ketol + C6-diol, fuscumol + fuscumol acetate, solvent control (1 July–21 August 2010, 51 d) |
| Near Black Butte, Sisters Ranger Dist., Deschutes Natl. For., Jefferson Co. | 44.370, −121.625 | Mixed hardwood | |
| Redwood Trail, Gold Beach Ranger Dist., Rogue River-Siskiyou Natl. For., Curry Co. | 42.117, −124.196 | Mature conifer with hardwood understory | |

Study sites are ordered so as to progress from states in the northeast to the midwest, south, and west. Abbreviations for chemicals: C6-ketol = racemic 3-hydroxyhexan-2-one, C8-ketol = racemic 3-hydroxyoctan-2-one, C10-ketol = racemic 3-hydroxydecan-2-one, *syn*-C6-diol = *syn*-2,3-hexanediol, *syn*-C8-diol = *syn*-2,3-octanediol, *anti*-C6-diol = *anti*-2,3-hexanediol, *anti*-C8-diol = *anti*-2,3-octanediol, C6-diol = *syn*- + *anti*-2,3-hexanediol.

lamiine pheromones fuscumol, fuscumol acetate, and monochamol. Blends of multiple components were included as treatments in some cases, because some cerambycid species are attracted only to synergistic blends of pheromone components, and not to the individual components (Millar and Hanks 2017). Furthermore, attraction of beetles to their synthesized pheromone often is not antagonized by pheromone components of other species, allowing the blending of pheromones of multiple species (Millar and Hanks 2017). Bioassays usually were set up in spring and continued through fall, for periods that ranged from 21 to 133 d (Table 1).

The number of treatments tested, the number of trap transects, and the duration of bioassays were subject to the resources available to the individual collaborators and their time constraints (Table 1). Experimental treatments were identical for USDA Forest Service collaborators in Vermont/New Hampshire, Louisiana, and Oregon, including C6-ketol, *syn*-C6-diol, *anti*-C6-diol, a blend of C6-ketol and all four stereoisomers of C6-diol, fuscumol blended with fuscumol acetate, and the solvent control. Bioassays in New York included the same treatments, but tested fuscumol and fuscumol acetate separately, and included both solvent and blank controls (empty lure). The bioassays in Indiana and Mississippi differed by including C8-ketols and diols, and monochamol. Two separate bioassays were conducted in Michigan, one comparing attraction to C6-, C8-, and C10-ketols (experiment 1), and the other comparing attraction to *syn*- and *anti*-C6- and C8-diols (experiment 2).

The same treatments were tested in Texas as at the other sites, including C6-ketol, *syn*-C6-diol, *anti*-C6-diol, fuscumol blended with fuscumol acetate, and monochamol, but included a ultra-high release ethanol treatment (release rate ~0.6 g/d; PheroTech Inc., Delta, BC, Canada), because that was the standard trap bait used by collaborator C.E.B. The Texas bioassays also differed in not having a solvent control. Instead, treatment effects were tested by using as controls those treatments that were known to be neutral as attractants for a particular species. For example, monochamol was used as a control for cerambycines because monochamol has only been shown to be a pheromone component or attractant for species in the subfamily Lamiinae. Similarly, the *syn*-C6-diol treatment was used as a control for lamiine species, because it only attracts species in the subfamilies Cerambycinae and Prioninae (Hanks and Millar 2016).

### Statistical Analysis

Overall treatment effects on attraction of individual species were tested separately for each study site using the nonparametric Friedman's test (PROC FREQ, option CMH; SAS Institute 2011) blocking by transect (if more than one) and collection date. Thus, all experiments were temporally replicated, and some also were spatially replicated. Replicates that contained no specimens of the species in question were not included in analyses, and data were analyzed only for species that were represented by at least ten specimens from the particular state. Assuming a significant overall Friedman's test, pairs of treatment means were compared with the REGWQ test (SAS Institute 2011).

Taxonomy of cerambycid beetles follows Monné and Hovore (2005), with the status of subfamilies based on Švácha and Lawrence (2014). Voucher specimens of species captured in New York have been submitted to the SUNY-ESF Insect Museum, Syracuse, and all specimens collected in Texas are at the Texas A&M University insect collection. For the remaining sites, voucher specimens are available from the individual collaborators with the exception of the Vermont, New Hampshire, and Oregon sites, for which voucher specimens were not retained.

## Results and Discussion

Traps at the various study sites caught a total of 12,800 beetles of the Cerambycidae and the related Disteniidae (Supplementary Table 1). The cerambycids included 153 species and subspecies including 50 species from 15 tribes in the Cerambycinae, 51 species from nine tribes in the Lamiinae, 39 species from three tribes of the Lepturinae, five species from four tribes of the Prioninae, five species from one tribe of the Spondylidinae, two species from one tribe of the Necydalinae, and one species of the Parandrinae. Also caught were 58 specimens of the disteniid species *Elytrimitatrix undata* (F.). The only exotic species was *Phymatodes testaceus* (L.), which was introduced into North America from Eurasia (Lingafelter 2007).

There were 71 cases of statistically significant treatment effects for 35 species across the states, with some of the more common species being attracted to the same compounds in several different states (Table 2; Supplementary Table 2). Species showing significant treatment effects included 18 species of cerambycines, 14 species of lamiines, one prionine species, one spondylidine species, and an unidentified species in the latter subfamily in the genus *Tetropium*. As expected, species whose pheromones were represented in the experimental treatments, and that were trapped in large numbers, were those showing significant treatment effects (i.e., cerambycines, lamiines, spondylidines, and prionines; Supplementary Tables 1 and 2). For those species whose pheromones were not represented, treatment effects were not significant, even with good sample size. For example, many adults of the lepturines *Gaurotes cyanipennis* (Say) and *Xestoleptura crassicornis* (LeConte) were captured across treatments, including controls, with no sign of significant attraction to any of the tested compounds. These diurnal species may have been drawn to traps by visual cues, such as a silhouette that resembles a tree trunk (Allison et al. 2014), regardless of whatever lures were deployed in the traps. Furthermore, even species whose pheromones were present in lures may have been caught in low numbers or not at all if bioassays at particular sites were conducted at the wrong time of year, or in the wrong habitats, or because population densities were naturally low. Thus, these bioassays offer only a one-sided test: a significant treatment effect for a species represents good evidence of attraction, but the lack of statistical significance provides no useful information about the chemical ecology of the species, because it is not known whether adults were active and abundant when traps were deployed.

Many of the species that were trapped previously had been shown to be attracted to one or more of the compounds deployed in the trials described here, and in some cases their pheromones had been identified by analysis of headspace odors from live beetles (summarized in Hanks and Millar 2016). For example, C6-ketol was known to be a dominant or sole pheromone component, or at least an attractant for the cerambycines (Table 2) *Cyrtophorus verrucosus* (Olivier), *Phymatodes aereus* (Newman), *P. testaceus*, *Neoclytus mucronatus mucronatus* (F), *Neoclytus scutellaris* (Olivier), *Xylotrechus colonus* (F.), and *Anelaphus pumilus* (Newman). Attraction of *Parelaphidion aspersum* (Haldeman) to C6-ketol confirms an earlier report that the males produce this compound along with 2-decanone (Mitchell et al. 2013). Species already known to have *syn*-C6-diol as a pheromone component included *Neoclytus acuminatus acuminatus* (F.) and *X. colonus*. Those known to use *anti*-C6-diol included *Megacyllene caryae* (Gahan), *Sarosesthes fulminans* (F.), and *Curius dentatus* Newman. During the bioassay in Texas, the only cerambycines that were attracted to traps baited with ethanol were *Knulliana cincta cincta* (Drury), which previously had been reported to respond to synergistic blends of ketols and ethanol (Miller et al. 2015b, 2017), and *Elaphidion mucronatum* (Say), which to our knowledge was not previously known to be attracted to ethanol.

The cerambycine *Obrium maculatum* (Olivier) apparently is unusual in being attracted to pheromones that are typical of lamiines and spondylidines. Adults of that species were attracted by fuscumol in the Mississippi bioassay (Table 2), but by fuscumol acetate, and not fuscumol, in an independent bioassay conducted in Texas (Mitchell et al. 2011). In the present article, bioassays in Texas showed that *O. maculatum* also was attracted by the blend

**Table 2.** Mean (±SE) number of cerambycid beetles captured per replicate during field bioassays in different states of the United States, and results of Friedman's *Q* analyses

| Subfamily/tribe | Taxonomy | State | Treatment | Mean ± SE | Control mean | *Q* (df)[a] |
|---|---|---|---|---|---|---|
| Cerambycinae | | | | | | |
| Anaglyptini | *Cyrtophorus verrucosus* | NY | C6-ketol | 1.44 ± 0.41 | 0.17 ± 0.1 | 38.1 (7,144)*** |
| Bothriospilini | ***Knulliana c. cincta*** | TX | Ethanol | 1.40 ± 0.34 | 0 | 43.0 (5,100)*** |
| Callidiini | ***Phymatodes aeneus*** | OR | C6-ketol | 7.7 ± 2.6 | 0 | 27.7 (5,42)*** |
| | *Phymatodes aereus* | NY | C6-ketol | 3.4 ± 2.2 | 0 | 38.9 (7,40)*** |
| | *Phymatodes testaceus* | NH/VT | C6-ketol | 19.7 ± 10.2 | 0 | 12.9 (5,18)* |
| | | MI-1 | C6- +C8-ketol | 2.2 ± 0.9 | 0 | 21.5 (5,41)*** |
| Clytini | *Megacyllene caryae* | TX | *anti*-C6-diol | 2.0 ± 0.6 | 0 | 52.3 (5,102)*** |
| | *Neoclytus a. acuminatus* | NH/VT | *syn*-C6-diol | 1.9 ± 0.55 | 0 | 28.6 (5,42)*** |
| | | NY | *syn*-C6-diol | 2.2 ± 0.4 | 0.025 ± 0.2 | 253 (7,326)*** |
| | | MI-2 | *syn*-C6-diol | 5.2 ± 0.76a | 0.067 ± 0.04b | 191.1 (6,315)*** |
| | | | *syn*-C6- +C8-diol | 4.2 ± 0.76a | | |
| | | IN | *syn*-C6-diol | 5.6 ± 0.7 | 0.072 ± 0.04 | 303 (9,561)*** |
| | | MS | *syn*-C6-diol | 21.1 ± 1.7 | 0.65 ± 0.3 | 83.5 (9,169)*** |
| | | LA | *syn*-C6-diol | 14.6 ± 2.8 | 0.23 ± 0.2 | 56.2 (5,81)*** |
| | | TX | *syn*-C6-diol | 33.0 ± 4.4 | 0.086 ± 0.05 | 98.0 (5,209)*** |
| | *Neoclytus m. mucronatus* | NY | C6-ketol | 5.0 ± 1.1 | 0 | 44.0 (7,64)*** |
| | | MI-1 | C6- +C8-ketol | 2.7 ± 0.6a | 0.017 ± 0.01b | 64.7 (5,108)*** |
| | | | C6-ketol | 1.6 ± 0.7a | | |
| | | MI-2 | *anti*-C6-diol | 1.2 ± 0.26 | 0 | 26.8 (6,49)*** |
| | | IN | C6-ketol | 4.2 ± 0.9 | 0.056 ± 0.05 | 130 (9,187)*** |
| | | LA | C6-ketol | 2.1 ± 0.7 | 0.10 ± 0.10 | 19.0 (5,60)** |
| | | MS | C6-ketol | 6.9 ± 2.7 | 0.25 ± 0.1 | 46.8 (9,159)*** |
| | | TX | C6-ketol | 10.1 ± 3.0 | 0.52 ± 0.2 | 33.5 (5,197)*** |
| | *Neoclytus scutellaris* | LA | C6-ketol | 9.9 ± 3.0 | 1.5 ± 0.6 | 15.3 (5,78)** |
| | | TX | C6-ketol | 2.1 ± 0.4 | 0.09 ± 0.09 | 52.7 (5,66)*** |
| | *Rusticoclytus a. emotus* | OR | C6-ketol+C6-diol | 3.0 ± 1.1 | 0 | 11.4 (5,18)* |
| | *Sarosesthes fulminans* | IN | *anti*-C6-diol | 3.53 ± 1.1 | 0 | 124 (9,187)*** |
| | *Xylotrechus colonus* | NH/VT | C6-ketol | 3.5 ± 0.79a | 0.38 ± 0.2c | 38.3 (5,78)*** |
| | | | C6-ketol+C6-diol | 2.46 ± 0.84ab | | |
| | | NY | C6-ketol | 4.4 ± 0.8 | 0.03 ± 0.03 | 183.0 (7,272)*** |
| | | MI-1 | C6-ketol | 1.48 ± 0.26a | 0.069 ± 0.05c | 55.0 (5,174)*** |
| | | | C6- +C8-ketol | 0.79 ± 0.2b | | |
| | | MI-2 | *anti*-C6-diol | 1.2 ± 0.3 | 0 | 21.7 (6,42)** |
| | | IN | C6-ketol | 7.83 ± 1.2a | 0.13 ± 0.1c | 202 (9,551)*** |
| | | | *anti*-C6-diol | 2.1 ± 0.3b | | |
| Curiini | *Curius dentatus* | LA | C6-ketol+C6-diol | 6.1 ± 1.4a | 0.14 ± 0.1b | 30.0 (5,42)*** |
| | | | *anti*-C6-diol | 5.7 ± 1.5a | | |
| | | MS | *anti*-C6-diol | 1.4 ± 0.04 | 0 | 37.9 (9,39)*** |
| Elaphidiini | *Anelaphus pumilus* | IN | C6-ketol | 2.5 ± 0.65 | 0 | 38.9 (9,40)*** |
| | | LA | C6-ketol | 10.2 ± 7.0 | 0.2 ± 0.2 | 13.0 (5,30)* |
| | ***Elaphidion mucronatum*** | MS | *anti*-C6-diol | 1.56 ± 0.3a | 0.44 ± 0.2c | 32.8 (9,159)*** |
| | | | Fuscumol | 1.4 ± 0.3ab | | |
| | | TX | Ethanol | 3.2 ± 0.7 | 071 ± 0.2 | 20.0 (5,208)** |
| | *Parelaphidion aspersum* | LA | C6-ketol | 2.2 ± 1.2 | 0.14 ± 0.1 | 16.0 (5,42)* |
| Obriini | *Obrium maculatum* | MS | Fuscumol | 2.7 ± 1.0 | 0.18 ± 0.1 | 24.4 (9,109)** |
| | | TX | Fuscumol+acetate | 7.4 ± 2.1 | 1.8 ± 1.0 | 22.2 (5,178)*** |
| Trachyderini | ***Ancylocera bicolor*** | LA | C6-ketol+C6-diol | 6.1 ± 2.0 | 0 | 48.4 (5,66)*** |
| | | TX | *anti*-C6-diol | 1.6 ± 0.2 | 0 | 56.0 (5,66)*** |
| Lamiinae | | | | | | |
| Acanthocinini | *Astyleiopus variegatus* | LA | Fuscumol+acetate | 2.4 ± 0.5 | 0 | 28.7 (5,3)*** |
| | *Astylidius parvus* | IN | Fuscumol | 3.0 ± 0.3 | 0 | 163 (9,165)*** |
| | | TX | Ethanol | 1.3 ± 0.2 | 0.21 ± 0.09 | 42.5 (5,141)*** |
| | *Astylopsis macula* | NY | Fuscumol acetate | 1.3 ± 0.9a | 0.33 ± 0.2b | 27.7 (7,48)*** |
| | | | Fuscumol | 1.2 ± 0.2a | | |
| | *Graphisurus fasciatus* | NY | Fuscumol acetate | 2.4 ± 0.63 | 0.05 ± 0.05 | 86.8 (7,160)*** |
| | | IN | Fuscumol acetate | 1.57 ± 0.3 | 0.05 ± 0.05 | 77.3 (9,207)*** |
| | *Lepturges angulatus* | NY | Fuscumol acetate | 1.75 ± 1.1 | 0 | 18.9 (7,32)* |
| | | TX | Fuscumol+acetate | 3.2 ± 0.8 | 0.13 ± 0.07 | 50.3 (5,142)*** |
| | ***Lepturges confluens*** | NY | Fuscumol acetate | 2.3 ± 0.88 | 0.33 ± 0.3 | 16.4 (7,24)* |
| | | MS | Fuscumol acetate | 2.5 ± 1.2 | 0 | 23.2 (9,40)** |
| | *Sternidius alpha* | NY | Fuscumol | 1.4 ± 0.34 | 0 | 81.4 (7,128)*** |
| | | IN | Fuscumol | 1.9 ± 0.9 | 0 | 112 (9,159)*** |

(*Continued*)

**Table 2.** Continued.

| Subfamily/tribe | Taxonomy | State | Treatment | Mean ± SE | Control mean | $Q$ (df)[a] |
|---|---|---|---|---|---|---|
| | | LA | Fuscumol+acetate | 24.8 ± 6.4 | 0.36 ± 0.2 | 32.4 (5,69)*** |
| | | TX | Fuscumol+acetate | 5.7 ± 2.0 | 0.27 ± 0.1 | 27.1 (5,132)*** |
| | ***Sternidius misellus*** | LA | Fuscumol+acetate | 16.4 ± 6.0 | 0 | 31.2 (5,63)** |
| | ***Styloleptus b. biustus*** | TX | Ethanol | 2.2 ± 0.6a | 0.44 ± 0.4b | 61.2 (5,191)*** |
| | | | Fuscumol+acetate | 1.7 ± 0.5a | | |
| Acanthoderini | ***Aegomorphus modestus*** | NY | Fuscumol acetate | 1.33 ± 0.18 | 0 | 70.7(7,72)*** |
| | | IN | Fuscumol acetate | 2.4 ± 0.6 | 0.17 ± 0.1 | 77.0 (9,119)*** |
| | ***Urgleptes signatus*** | NH/VT | Fuscumol+acetate | 0.83 ± 0.16 | 0 | 18.1 (5,36)* |
| | | NY | Fuscumol acetate | 1.0 ± 0 | 0 | 32.9 (7,40)*** |
| Dorcaschematini | *Dorcaschema alternatum* | TX | *anti*-C6-diol | 1.6 ± 0.2 | 0.2 ± 0.2 | 20.0 (5,30)** |
| Pogonocherini | ***Ecyrus d. dasycerus*** | LA | Fuscumol+acetate | 1.4 ± 0.5 | 0.5 ± 0.4 | 11.4 (5,60)* |
| | | MS | Fuscumol | 1.50 ± 0.4 | 0 | 36.6 (9,100)*** |
| | | TX | Ethanol | 1.6 ± 0.4 | 0.077 ± 0.05 | 36.2 (5,156)*** |
| Pteropliini | ***Ataxia crypta*** | TX | Ethanol | 1.2 ± 0.3 | 0.32 ± 0.2 | 29.1 (5,114)*** |
| Prioninae | | | | | | |
| Meroscelisini | *Tragosoma depsarium* | OR | *syn*-C6-diol | 5.1 ± 4.1 | 0 | 16.8 (5,42)** |
| Spondylidinae | | | | | | |
| Asemini | ***Asemum striatum*** | NH/VT | Fuscumol+acetate | 1.3 ± 0.6 | 0.25 ± 0.2 | 12.9 (5,24)* |
| | | NY | Fuscumol | 1.6 ± 0.39 | 0.09 ± 0.09 | 29.5 (7,88)*** |
| | *Tetropium* spp. | NH/VT | Fuscumol+acetate | 3.2 ± 0.78 | 0.33 ± 0.1 | 30.0 (5,72)*** |
| | | NY | Fuscumol | 6.5 ± 1.3 | 0.09 ± 0.05 | 145.5 (7,264)*** |

Only means for statistically significant treatments and controls are presented. When more than one treatment attracted significantly more beetles than the control, significant differences between treatments are shown with different letters (REGWQ test, $P < 0.05$). See Supplementary Table 2 for means of all the treatments. Abbreviations for chemicals as in Table 1, with the exception fuscumol+acetate = fuscumol + fuscumol acetate. Species in bold text indicate new information about attractants. Asterisks indicate significance level of Friedman's $Q$ for overall treatment effects: $*P < 0.01$; $**P < 0.001$; $***P < 0.0001$.

of fuscumol and fuscumol acetate, as was true in another study conducted in Pennsylvania (Hanks and Millar 2013), but in both cases the individual components had not been tested separately. Attraction of *O. maculatum* to fuscumol in one part of its range, and to fuscumol acetate in another part, suggests that there may be geographic races of this species that differ in their response profiles. To date, it is not known whether either sex of *O. maculatum* produces attractant pheromones, and there is no evidence that this species responds to any of the known pheromones of cerambycines.

Several cerambycine species with no documented attractants were significantly attracted to test treatments in this study, providing leads to their possible pheromones. Examples include the attraction of *Phymatodes aeneus* LeConte, *Rusticoclytus annosus emotus* (Brown), *E. mucronatum*, and *Ancylocera bicolor* (Olivier) to traps baited with C6-ketols, or *syn*- and *anti*-C6-diols (in some cases binary blends of these compounds; Table 2). The finding that *E. mucronatum* was attracted by *anti*-C6-diol was unexpected, because this species recently has been found to have a single-component pheromone with a structure entirely different from those of any of the compounds tested, (2*E*,6*Z*,9*Z*)-2,6,9-pentadecatrienal (Millar et al. 2017). Also surprising was attraction of *N. m. mucronatus* by *anti*-C6-diol in Michigan, because the pheromone of that species is comprised solely of 3*R*-C6-ketol (Lacey et al. 2007), and there had been no sign of attraction of this species to the diol in earlier studies (e.g., Hanks et al. 2012, Hanks and Millar 2013). Another unexpected finding was attraction of *M. caryae* to *anti*-C6-diol at study sites in Texas, because beetles of this species were attracted only to *syn*-C6-diol in independent bioassays conducted in Pennsylvania and Illinois (Hanks and Millar 2013, L.M.H. unpublished data). The latter finding was also surprising because only the *anti*-diols are components of the pheromone produced by males of that species in east-central Illinois (Lacey et al. 2008). Attraction to the *anti*-diol in Texas and *syn*-diol elsewhere again suggests that geographically separated populations of *M. caryae* may differ in their response profiles, or even in which diastereomers the males produce.

Responses of beetles to binary blends of different pheromone structures at many of the study sites provided evidence of synergism, and in some cases antagonism among components. For example, the exotic species *P. testaceus* was significantly attracted only by the blend of C6- and C8-ketols in Michigan, and not to the individual components, even though it was attracted by C6-ketol alone in the absence of the blend during bioassays in New Hampshire and Vermont (Supplementary Table 2). Similarly, adults of *A. bicolor* were significantly attracted by the blend of C6-ketol and all four 2,3-hexanediol stereoisomers in Louisiana, but to *anti*-C6-diol alone in bioassays in Texas that lacked the ketol/diol blend. These findings suggest that even weak attraction to certain pheromone components can result in statistically significant treatment effects when more powerful attractants are not included in bioassays. In addition, adults of *X. colonus* were attracted to *anti*-C6-diol during bioassays in Michigan which included only diols of varying stereochemistry and chain length, but not in any other bioassay that included the strong attractant C6-ketol. The pheromone of *X. colonus* is composed primarily of the ketol, with all four diol enantiomers as minor components (Lacey et al. 2009, L.M.H. unpublished data), but earlier studies had suggested that neither of the diols was significantly attractive by itself, even in the absence of traps baited with the ketol (Wong et al. 2017).

Attraction of the cerambycine *N. a. acuminatus* to its pheromone (2*S*,3*S*)-C6-diol was strongly antagonized by the C6-ketol at study sites where that blend was tested (New Hampshire/Vermont, Louisiana; Table 2). The antagonistic effect of the ketol for this species had been reported in earlier publications (Hanks et al. 2012, Hanks and Millar 2013, Miller et al. 2017), and may be adaptive because it would serve to prevent the adults from responding to (2*S*,3*S*)-C6-diol in the pheromones of other species. One such species

is *X. colonus*, which overlaps broadly in seasonal and daily activity periods with *N. a. acuminatus*, and is similarly abundant (Hanks et al. 2014; L.M.H. unpublished data). Attraction to C6-ketol was antagonized by C8-ketol for *X. colonus* in Michigan, and by C6-diols for *N. scutellaris* in Louisiana and *P. aeneus* in Oregon.

Consistent with the findings reported here, several lamiine species already were known to be attracted by fuscumol and/or fuscumol acetate, including *Astyleiopus variegatus* (Haldeman), *Astylidius parvus* (LeConte), *Astylopsis macula* (Say), *Graphisurus fasciatus* (Degeer), *Lepturges angulatus* (LeConte), *Lepturges confluens* (Haldeman), *Sternidius alpha* (Say), and *Aegomorphus modestus* (Gyllenhal) (summarized in Hanks and Millar 2016). It should be noted that attraction to the blend of the two compounds may be misleading where they were not also tested individually. For example, adults of *L. angulatus* were attracted to the blend of fuscumol and fuscumol acetate at study sites in Texas, where the compounds were not tested separately, but the bioassay in New York, in which the two components were tested separately, revealed that only the acetate was significantly attractive as a single component (Table 2). Recent research has confirmed that the pheromones of *A. variegatus*, *A. parvus*, and *L. angulatus* are composed of species-specific combinations of the enantiomers of fuscumol and fuscumol acetate (Hughes et al. 2013, 2016; Meier et al. 2016). Extending this list of species, attraction to fuscumol and/or fuscumol acetate in the present study provides the first clues to the likely pheromone chemistries of the lamiine species *Sternidius misellus* (LeConte), *Styloleptus biustus biustus* (LeConte), *Urgleptes signatus* (LeConte), and *Ecyrus dasycerus dasycerus* (Say). The Texas bioassay further revealed that ethanol alone attracted significant numbers of the lamiines *A. parvus*, *S. b. biustus*, *E. d. dasycerus,* and *Ataxia crypta* (Say).

Much like the unusual attraction of the cerambycine *O. maculatum* to the lamiine pheromones fuscumol or fuscumol acetate, the lamiine *Dorcaschema alternatum* (Say) was attracted by a typical pheromone component of cerambycines, *anti*-C6-diol, at study sites in Texas (Table 2). Attraction to the same compound also was found in an independent field experiment in Pennsylvania (Hanks and Millar 2013).

It should also be noted that the bioassays in New York showed that the lamiines *Monochamus scutellatus scutellatus* (Say) and its congener *M. notatus* (Drury) were significantly attracted by monochamol, however, those data already have been published (Fierke et al. 2012). That article also confirmed that males of *M. s. scutellatus* do indeed produce monochamol.

Significant treatment effects for the remaining species in the smaller subfamilies also were consistent with previous work (Table 2). Based on its attraction to *syn*-C6-diol, it seems likely that the prionine identified as *Tragosoma depsarium* (L.) was actually *T. depsarium* 'sp. nov. Laplante' (Ray et al. 2012). From the subfamily Spondylidinae, a *Tetropium* species was attracted by fuscumol as a single component. Other species in this genus are known to use fuscumol as a pheromone, but apparently are only strongly attracted to it when synergized by host plant volatiles (Silk et al. 2007, Sweeney et al. 2010). Finally, this is the first report that the spondylidine *Asemum striatum* (L.) is attracted to fuscumol. It had previously been reported to be attracted only by plant volatiles (Miller et al. 2011, 2015a; Hanks and Millar 2013), or by a combination of a generic blend which contained fuscumol and fuscumol acetate, among other components, along with α-pinene (Collignon et al. 2016).

In summary, the results reported here provide further evidence of the value of field screening bioassays as a tool for initiating research on the chemical ecology of cerambycid beetles in general, and certain species in particular. Follow-up studies can target any species which are attracted to any of the lures deployed, particularly because live trapping of species in the subfamilies Cerambycinae, Lamiinae, and Spondylidinae typically provides specimens of both sexes. Collection and analysis of the odors released by live beetles of both sexes can then be used to confirm that the beetles produce the compounds to which they were attracted, and that production of the compounds is male-specific. Moreover, it is likely that many more species could be targeted by carrying out similar field screening studies in different habitats and geographic regions, either in North America or on other continents (e.g., Sweeney et al. 2014, Wickham et al. 2014, Ryall et al. 2015, Hayes et al. 2016). The diversity of species that could be targeted also may be increased by sampling over the entire flight season, in order to have traps deployed during the successive seasonal activity periods of many species, as well as deploying traps at different heights within forest canopies (Millar and Hanks 2017).

## Supplementary Material

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

## Acknowledgments

We thank the following agencies and people for access to field sites, and for logistical and technical assistance in the field and laboratory: in New Hampshire and Vermont, the Urban Forestry Center, Portsmouth NH (Angela Hammond), Green Mountain National Forest, VT (Chris Casey) and Northeastern Area, Durham, NH (Garret D. Dubois and Kevin J. Dodds); in New York, SUNY-ESF, New York State Parks, and the New York Department of Environmental Conservation; in Michigan, the MSU Tree Research Center (Paul Bloese), and Tom Baweja, Tina Ciaramitaro, and Thomas Rachman; in Indiana, Gary Frazier, Gabriel Hughes, Nicole Jeffers, and Matthew Paschen; in Mississippi, Nathan Schiff and Matthew Paschen; in Louisiana, Billy Bruce, Chris Steiner, the Roy O. Martin Lumber Co., LLC, and the Kisatchie National Forest Cathoula Ranger Dist.; in Texas, Julia Smith; and in Oregon, Paul Deignan, Andy Eglitis, Don Goheen, Jim LaBonte, Sundi Sigrist, and Elizabeth Willhite. Thanks also to R. J. Rabaglia (USDA Forest Service, Washington, DC) for help in finding collaborations with the USDA Forest Service. This research was supported by funding from The Alphawood Foundation of Chicago (to L.M.H.), and the National Research Initiative of the USDA Cooperative State Research, Education and Extension Service, grant number 2009-35302-05047 (to J.G.M. and L.M.H.).

## References Cited

**Allison, J. D., B. D. Bhandari, J. L. McKenney, and J. G. Millar. 2014.** Design factors that influence the performance of flight intercept traps for the capture of longhorned beetles (Coleoptera: Cerambycidae) from the subfamilies Lamiinae and Cerambycinae. Plos One. 9: e93203.

**Collignon, R. M., I. P. Swift, Y. Zou, J. S. McElfresh, L. M. Hanks, and J. G. Millar. 2016.** The influence of host plant volatiles on the attraction of longhorn beetles to pheromones. J. Chem. Ecol. 42: 215–229.

**Fierke, M. K., D. D. Skabeikis, J. G. Millar, S. A. Teale, J. S. McElfresh, and L. M. Hanks. 2012.** Identification of a male-produced aggregation pheromone for *Monochamus scutellatus scutellatus* and an attractant for the congener *Monochamus notatus* (Coleoptera: Cerambycidae). J. Econ. Entomol. 105: 2029–2034.

**Graham, E. E., R. F. Mitchell, P. F. Reagel, J. D. Barbour, J. G. Millar, and L. M. Hanks. 2010.** Treating panel traps with a fluoropolymer enhances their efficiency in capturing cerambycid beetles. J. Econ. Entomol. 103: 641–647.

**Hanks, L. M., and J. G. Millar. 2013.** Field bioassays of cerambycid pheromones reveal widespread parsimony of pheromone structures, enhancement by host plant volatiles, and antagonism by components from heterospecifics. Chemoecology 23: 21–44.

**Hanks, L. M., and J. G. Millar. 2016**. Sex and aggregation-sex pheromones of cerambycid beetles: basic science and practical applications. J. Chem. Ecol. 42: 631–654.

**Hanks, L. M., J. G. Millar, J. A. Moreira, J. D. Barbour, E. S. Lacey, J. S. McElfresh, F. R. Reuter, and A. M. Ray. 2007**. Using generic pheromone lures to expedite identification of aggregation pheromones for the cerambycid beetles *Xylotrechus nauticus*, *Phymatodes lecontei*, and *Neoclytus modestus modestus*. J. Chem. Ecol. 33: 889–907.

**Hanks, L. M., J. G. Millar, J. A. Mongold-Diers, J.C.H. Wong, L. R. Meier, P. F. Reagel, and R. F. Mitchell. 2012**. Using blends of cerambycid beetle pheromones and host plant volatiles to simultaneously attract a diversity of cerambycid species. Can. J. For. Res. 42: 1050–1059.

**Hanks, L. M., P. F. Reagel, R. F. Mitchell, J. C. Wong, L. R. Meier, C. A. Silliman, E. E. Graham, B. L. Striman, K. P. Robinson, J. A. Mongold-Diers, et al. 2014**. Seasonal phenology of the cerambycid beetles of east-central Illinois. Ann. Entomol. Soc. Am. 107: 211–226.

**Hayes, R. A., M. W. Griffiths, H. F. Nahrung, P. A. Arnold, L. M. Hanks, and J. G. Millar. 2016**. Optimizing generic cerambycid pheromone lures for Australian biosecurity and biodiversity monitoring. J. Econ. Entomol. 109: 1741–1749.

**Hughes, G. P., Y. Zou, J. G. Millar, and M. D. Ginzel. 2013**. (*S*)-Fuscumol and (*S*)-fuscumol acetate produced by a male *Astyleiopus variegatus* (Coleoptera: Cerambycidae). Can. Entomol. 145: 327–332.

**Hughes, G. P., L. R. Meier, Y. Zou, J. G. Millar, L. M. Hanks, and M. D. Ginzel. 2016**. Stereochemistry of fuscumol and fuscumol acetate influences attraction of longhorned beetles (Coleoptera: Cerambycidae) of the subfamily lamiinae. Environ. Entomol. 45: 1271–1275.

**Lacey, E. S., M. D. Ginzel, J. G. Millar, and L. M. Hanks. 2004**. Male-produced aggregation pheromone of the cerambycid beetle *Neoclytus acuminatus acuminatus*. J. Chem. Ecol. 30: 1493–1507.

**Lacey, E. S., J. A. Moreira, J. G. Millar, A. M. Ray, and L. M. Hanks. 2007**. Male-produced aggregation pheromone of the cerambycid beetle *Neoclytus mucronatus mucronatus*. Entomol. Exp. Appl. 122: 171–179.

**Lacey, E. S., J. A. Moreira, J. G. Millar, and L. M. Hanks. 2008**. A male-produced aggregation pheromone blend consisting of alkanediols, terpenoids, and an aromatic alcohol from the cerambycid beetle *Megacyllene caryae*. J. Chem. Ecol. 34: 408–417.

**Lacey, E. S., J. G. Millar, J. A. Moreira, and L. M. Hanks. 2009**. Male-produced aggregation pheromones of the cerambycid beetles *Xylotrechus colonus* and *Sarosesthes fulminans*. J. Chem. Ecol. 35: 733–740.

**Lingafelter, S. W. 2007**. Illustrated key to the longhorned woodboring beetles of the eastern United States. Coleopterists Society Miscellaneous Publication. Special Publication No. 3. Coleopterists Society, North Potomac, MD.

**Meier, L. R., Y. Zou, J. G. Millar, J. A. Mongold-Diers, and L. M. Hanks. 2016**. Synergism between enantiomers creates species-specific pheromone blends and minimizes cross-attraction for two species of cerambycid beetles. J. Chem. Ecol. 42: 1181–1192.

**Millar, J. G., and L. M. Hanks. 2017**. Chemical ecology of cerambycids, pp. 161–196. *In* Q. Wang (ed.) Cerambycidae of the world: biology and pest management. CRC Press/Taylor & Francis, Boca Raton, FL.

**Millar, J. G., R. F. Mitchell, J. A. Mongold-Diers, L. R. Meier, T. D. Johnson, and L. M. Hanks. 2018**. (2*E*,6*Z*,9*Z*)-2,6,9-pentadecatrienal as a male-produced aggregation-sex pheromone of the cerambycid beetle *Elaphidion mucronatum*. J. Chem. Ecol. 111: 252–259.

**Miller, D. R., C. Asaro, C. M. Crowe, and D. A. Duerr. 2011**. Bark beetle pheromones and pine volatiles: attractant kairomone lure blend for longhorn beetles (Cerambycidae) in pine stands of the southeastern United States. J. Econ. Entomol. 104: 1245–1257.

**Miller, D. R., C. M. Crowe, K. J. Dodds, L. D. Galligan, P. de Groot, E. R. Hoebeke, A. E. Mayfield, 3rd, T. M. Poland, K. F. Raffa, and J. D. Sweeney. 2015a**. Ipsenol, ipsdienol, ethanol, and α-pinene: trap lure blend for cerambycidae and buprestidae (coleoptera) in pine forests of Eastern North America. J. Econ. Entomol. 108: 1837–1851.

**Miller, D. R., C. M. Crowe, P. D. Mayo, P. J. Silk, and J. D. Sweeney. 2015b**. Responses of cerambycidae and other insects to traps baited with ethanol, 2,3-hexanediol, and 3,2-hydroxyketone lures in North-Central Georgia. J. Econ. Entomol. 108: 2354–2365.

**Miller, D. R., C. M. Crowe, P. D. Mayo, L. S. Reid, P. J. Silk, and J. D. Sweeney. 2017**. Interactions between ethanol, syn-2,3-hexanediol, 3-hydroxyhexan-2-one, and 3-hydroxyoctan-2-one lures on trap catches of hardwood longhorn beetles in southeastern United States. J. Econ. Entomol. 110: 2119–2128.

**Mitchell, R. F., E. E. Graham, J. C. H. Wong, P. F. Reagel, B. L. Striman, G. P. Hughes, M. A. Paschen, M. D. Ginzel, J. G. Millar, and L. M. Hanks. 2011**. Fuscumol and fuscumol acetate are general attractants for many species of cerambycid beetles in the subfamily Lamiinae. Entomol. Exp. Appl. 141: 71–77.

**Mitchell, R. F., J. G. Millar, and L. M. Hanks. 2013**. Blends of (*R*)-3-hydroxyhexan-2-one and alkan-2-ones identified as potential pheromones produced by three species of cerambycid beetles. Chemoecology 23: 121–127.

**Monné, M. A., and F. T. Hovore. 2005**. Checklist of the cerambycidae (coleoptera) of the western hemisphere. BioQuip, Rancho Dominguez, CA.

**Ray, A. M., A. Zunič, R. L. Alten, J. S. McElfresh, L. M. Hanks, and J. G. Millar. 2011**. cis-Vaccenyl acetate, a female-produced sex pheromone component of *Ortholeptura valida*, a longhorned beetle in the subfamily Lepturinae. J. Chem. Ecol. 37: 173–178.

**Ray, A. M., J. D. Barbour, J. S. McElfresh, J. A. Moreira, I. Swift, I. M. Wright, A. Žunič, R. F. Mitchell, E. E. Graham, R. L. Alten, et al. 2012**. 2,3-Hexanediols as sex attractants and a female-produced sex pheromone for cerambycid beetles in the prionine genus *Tragosoma*. J. Chem. Ecol. 38: 1151–1158.

**Ryall, K., P. Silk, R. P. Webster, J. M. Gutowski, Q. Meng, Q., Y. Li, W. Gao, J. Fidgen, T. Kimoto, T. Scarr, and V. Mastro. 2015**. Further evidence that monochamol is attractive to *Monochamus* (Coleoptera: Cerambycidae) species, with attraction synergised by host plant volatiles and bark beetle (Coleoptera: Curculionidae) pheromones. Can. Entomol. 147: 564–579.

**SAS Institute. 2011**. SAS/STAT 9.3 user's guide. SAS Institute Inc., Cary, NC.

**Silk, P. J., J. Sweeney, J. Wu, J. Price, J. M. Gutowski, and E. G. Kettela. 2007**. Evidence for a male-produced pheromone in *Tetropium fuscum* (F.) and *Tetropium cinnamopterum* (Kirby) (Coleoptera: Cerambycidae). Naturwissenschaften. 94: 697–701.

**Silva, W. D., J. G. Millar, L. M. Hanks, and J. M. Bento. 2016a**. 10-methyldodecanal, a novel attractant pheromone produced by males of the South American cerambycid beetle *Eburodacrys vittata*. Plos One. 11: e0160727.

**Silva, W. D., J. G. Millar, L. M. Hanks, and J. M. Bento. 2016b**. (6*E*,8*Z*)-6,8-pentadecadienal, a novel attractant pheromone produced by males of the cerambycid beetles *Chlorida festiva* and *Chlorida costata*. J. Chem. Ecol. 42: 1082–1085.

**Švácha, P., and J. F. Lawrence. 2014**. Chapter 2.4 Cerambycidae Latreille, 1802, pp 77–177. *In* R. A. B. Leschen and R. G. Beutel (eds.), Handbook of zoology: Arthropoda: Insecta: Coleoptera, beetles. Vol. 3: morphology and systematics (Phytophaga). Walter de Gruyter, Berlin/Boston.

**Sweeney, J. D., P. J. Silk, J. M. Gutowski, J. Wu, M. A. Lemay, P. D. Mayo, and D. I. Magee. 2010**. Effect of chirality, release rate, and host volatiles on response of *Tetropium fuscum* (F.), *Tetropium cinnamopterum* Kirby, and *Tetropium castaneum* (L.) to the aggregation pheromone, fuscumol. J. Chem. Ecol. 36: 1309–1321.

**Sweeney, J. D., P. J. Silk, and V. Grebennikov. 2014**. Efficacy of semiochemical-baited traps for detection of longhorn beetles (Coleoptera: Cerambycidae) in the Russian Far East. Eur. J. Entomol. 111: 397–406.

**Wickham, J. D., R. D. Harrison, W. Lu, Z. Guo, J. G. Millar, L. M. Hanks, and Y. Chen. 2014**. Generic lures attract cerambycid beetles in a tropical montane rain forest in southern China. J. Econ. Entomol. 107: 259–267.

**Wickham, J. D., W. Lu, L. W. Zhang, Y. Chen, Y. Zou, L. M. Hanks, and J. G. Millar. 2016**. Likely aggregation-sex pheromones of the invasive beetle *Callidiellum villosulum*, and the related asian species *Allotraeus asiaticus*, *Semanotus bifasciatus*, and *Xylotrechus buqueti* (Coleoptera: Cerambycidae). J. Econ. Entomol. 109: 2243–2246.

**Wong, J.C.H., L. R. Meier, Y. Zou, J. A. Mongold-Diers, and L. M. Hanks. 2017**. Evaluation of methods used in testing attraction of cerambycid beetles to pheromone-baited traps. J. Econ. Entomol. 110: 2269–2274.

**Zou, Y., J. G. Millar, J. S. Blackwood, R. Van Duzor, L. M. Hanks, J. A. Mongold-Diers, J.C.H. Wong, and A. M. Ray. 2015**. (2*S*,4*E*)-2-Hydroxy-4-octen-3-one, a male-produced attractant pheromone of the cerambycid beetle *Tylonotus bimaculatus*. J. Chem. Ecol. 41: 670–677.