Generic Lures Attract Cerambycid Beetles in a Tropical Montane Rain Forest in Southern China

JACOB D. WICKHAM,[1] RHETT D. HARRISON,[2] WEN LU,[3] ZHENPENG GUO,[1]
JOCELYN G. MILLAR,[4] LAWRENCE M. HANKS,[5,6] AND YI CHEN[1,6]

J. Econ. Entomol. 107(1): 259–267 (2014); DOI: http://dx.doi.org/10.1603/EC13333

ABSTRACT The attraction of cerambycid beetles to 10 known cerambycid pheromones was tested in a tropical montane rain forest in southern China. From 28 May to 25 June 2010, 1,526 cerambycids representing 71 species were captured in pheromone-baited traps, with 14 species accounting for 92% of the specimens. Test compounds with a 3-hydroxyalkan-2-one or 2,3-alkanediol motif attracted significant numbers of both sexes for eight species in the subfamily Cerambycinae, including species of *Demonax*, *Rhaphuma*, and *Xylotrechus*. *Rhaphuma horsfieldi* (White) was the only species that was strongly attracted to more than one test compound, with significant attraction to both (2*R**,3*R**)-2,3-hexanediol and (2*R**,3*R**)-2,3-octanediol. Within the Lamiinae, males and females of five species were significantly attracted to 2-(undecyloxy)ethanol, including *Acalolepta formosana* (Breuning), *Monochamus bimaculatus* Gahan, *Pharsalia subgemmata* (Thomson), *Pseudomacrochenus antennatus* (Gahan), and *Xenohammus bimaculatus* Schwarzer. Only male *Megopis costipennis* White (Prioninae) were significantly attracted to (2*R**,3*S**)-2,3-octanediol, suggesting that this compound may be a sex pheromone component for this species. To date, 2,3-octanediols have only been reported as aggregation pheromone components for cerambycids in the subfamily Cerambycinae. Our results support the hypothesis that both closely related (congeners) and more distantly related cerambycid species (different tribes and even subfamilies) may share pheromone components. Our results also demonstrate that traps baited with even a limited number of different classes of pheromones may be useful tools for surveying cerambycid diversity, as well as for detecting and monitoring particular species, especially those that have the potential to be invasive pests in other parts of the world.

KEY WORDS Cerambycidae, pheromone, attractant, longhorned beetle

Cerambycid beetles play many important ecological roles in forest ecosystems. Their larvae generally feed cryptically within woody tissues and have prolonged development times ranging from months to several years (Linsley 1961). The larvae and pupae are readily transported in wooden products, packing materials, and dunnage, providing a major pathway for introduction of exotic wood-boring species into new areas of the world as a consequence of global trade (Brockerhoff et al. 2006, Haack 2006). This problem is compounded by the difficulty in detecting the immature stages of exotic species at ports of entry (Haack et al. 2010) and by the lack of effective and efficient methods of monitoring for adult beetles, such as the use of pheromone-baited traps.

Although there is extensive literature on the geographic ranges of cerambycid species and the host associations of the larvae (Duffy 1953, 1968; volumes indexed in Linsley and Chemsak 1997; Tavakilian et al. 1997), much less is known about the biology of adult beetles, particularly the semiochemically mediated mechanisms involved in host selection and mate location. Recent advances in the identification of cerambycid pheromones have resulted in the development and optimization of methods for using pheromone-based attractants to detect many cerambycid species and characterize local cerambycid communities (Graham et al. 2010, Allison et al. 2011, Mitchell et al. 2011, Graham et al. 2012, Hanks and Millar 2013). These studies suggest that there is a general trend within the Cerambycidae for aggregation pheromones to be produced by males (i.e., pheromones that attract both sexes; Millar et al. 2009), whereas sex attractant pheromones are produced by females, and attract only males (Barbour et al. 2011; Ray et al. 2011, 2012). Pheromone structures also appear to be highly conserved among closely related cerambycid species. For example, pheromones of many species in the subfam-

---

[1] Key Laboratory of Analytical Chemistry for Living Biosystems, Institute of Chemistry, Chinese Academy of Sciences, Beijing 100190, China.

[2] First North Street, Haidian District, Beijing 100190, China.

[3] Department of Plant Protection, College of Agriculture, Guangxi University, 100 Daxue Road, Nanning, Guangxi 530005, China.

[4] Department of Entomology, University of California, 3401 Watkins Drive, Riverside, CA 92521.

[5] Department of Entomology, University of Illinois at Urbana-Champaign, 320 Morrill Hall, 505 South Goodwin Avenue, Urbana, IL 61801.

[6] Corresponding authors, e-mails: hanks@life.illinois.edu; chenyi@iccas.ac.cn.

ily Cerambycinae are composed of 6- to 10-carbon 3-hydroxyalkan-2-ones, 2-hydroxyalkan-3-ones, or 2,3-alkanediols (Hanks and Millar 2013), whereas those of species in the subfamily Lamiinae (including species of *Monochamus* and *Anoplophora glabripennis* [Motschulsky]) consist of hydroxyethers and related compounds (Zhang et al. 2002, Pajares et al. 2010, Teale et al. 2011, Allison et al. 2012, Fierke et al. 2012, Macias-Samano et al. 2012). For the subfamily Spondylidinae and some species in the subfamily Lamiinae, the terpenoid (*E*)-6,10-dimethylundeca-5,9-dien-2-ol (hence fuscumol) and its corresponding acetate constitute pheromone components that are shared by a number of species (Silk et al. 2007, Fonseca et al. 2010, Mitchell et al. 2011). Recent large-scale screening studies also have shown that several sympatric species may be attracted to a single pheromone compound (Hanks et al. 2007, Mitchell et al. 2011, Graham and Poland 2012, Hanks and Millar 2013).

We report the results from testing 10 known cerambycid pheromone components in the newly created Bulong Nature Reserve in southern Yunnan province, China. The tropical montane rain forest habitat is considered a biodiversity hotspot (Wang et al. 2000, Xu et al. 2009), and data resulting from the work reported here will provide a valuable contribution to ongoing biodiversity surveys within the reserve. Because previous studies have shown that there appears to be extensive biosynthetic parsimony in cerambycid pheromones, with a single compound being used as a pheromone component by a number of related species, we predicted 1) that the 2,3-alkanediol and 3-hydroxyalkan-2-one structural motifs would attract species of the Cerambycinae, 2) that hydroxyethers would attract species of the Lamiinae, and 3) that fuscumol and/or fuscumol acetate would attract species of the Lamiinae and Spondylidinae. The relatively large number of species (71, see further text) caught in the pheromone-baited traps during the 1-mo period of the field assays demonstrates the potential for using such traps as tools for surveying biodiversity of cerambycids in their natural habitats, and for detecting potentially invasive Asian species, as they are transported around the world by global trade.

Materials and Methods

Test compounds were prepared by previously described methods as racemic mixtures (i.e., 1:1 mixtures of the two enantiomeric forms). For the diols with two chiral centers, the relative configurations are shown with the (*R*)- or (*S*)-designation followed by asterisks to indicate that the compounds are diastereomerically pure but mixtures of the two enantiomers. For example, (2*R**,3*R**)-2,3-hexanediol is a racemic mixture of the (2*R*,3*R*)- and (2*S*,3*S*)-enantiomers. The following compounds were tested: racemic 3-hydroxyhexan-2-one, 3-hydroxyoctan-2-one, and 3-hydroxydecan-2-one (Imrei et al. 2013); (2*R**,3*R**)- and (2*R**,3*S**)-2,3-hexanediols, and (2*R**,3*R**)- and (2*R**,3*S**)-2,3-octanediols (Lacey et al. 2004); 2-(undecyloxy)-ethanol (Pajares et al. 2010); 4-(heptyloxy)butan-1-ol and 4-(heptyloxy)butanal (Zhang et al. 2002); racemic (*Z*/*E*)-6,10-dimethyl-5,9-undecadien-2-ol and (*Z*/*E*)-6,10-dimethyl-5,9-undecadien-2-yl acetate as 4:5 mixtures of (*Z*)- and (*E*)-isomers (Mitchell et al. 2011). All compounds were synthesized at the University of California, Riverside (Riverside, CA).

The study site was a steeply sloped forest in the newly created Bulong Nature Reserve (21° 30′29.39″ N, 100° 29′50.60″ E; average elevation 1,625 m), at the southern tip of Yunnan province in China, and within 10 km of the Myanmar border. The reserve consists of a patchy landscape of both secondary and old growth forest interspersed with tea plantations and open landscapes, and is classified as a seasonal tropical montane rain forest (average temperatures 15–21°C). The field trapping experiment used 48 flight-intercept panel traps (1.2 m in height by 0.30 m in width, AlphaScents, Portland, OR) with the panels and lower funnel portions of the trap painted with undiluted Fluon to increase trapping efficiency (Graham et al. 2010, Graham and Poland 2012). Pheromone lures were clear, zip-seal polyethylene sachets (Cat. #018161A, 5.1 cm by 7.6 cm, Thermo-Fisher, Waltham, MA) loaded with 1 ml of an ethanol solution of a test compound.

The experiment was conducted from 28 May to 25 June 2010, and consisted of four blocks of the following treatments (assigned randomly to initial positions): 1) (2*R**,3*R**)-2,3-hexanediol (50 mg), 2) (2*R**,3*S**)-2,3-hexanediol (50 mg), 3) 3-hydroxyhexan-2-one (50 mg), 4) (2*R**,3*R**)-2,3-octanediol (50 mg), 5) (2*R**,3*S**)-2,3-octanediol (50 mg), 6) 3-hydroxyoctan-2-one (50 mg), 7) 3-hydroxydecan-2-one (50 mg), 8) 2-(undecyloxy)ethanol (25 mg), 9) (*Z*/*E*)-6,10-dimethyl-5,9-undecadien-2-ol (100 mg), and 10) (*Z*/*E*)-6,10-dimethyl-5,9-undecadien-2-ol acetate (100 mg). To control for possible solvent effects and passive capture of beetles, two different controls were used in each block: an unbaited trap and a trap baited with a sachet containing 1 ml of ethanol. Lures were suspended with wire at the center of traps. Traps were hung in trees with a minimum spacing of 10 m between traps, with trap basins ≈1 m above ground level. Basins were filled with a mixture of ethylene glycol and soapy water to retain and preserve captured beetles. Traps were rebaited with fresh lures and trap positions were rerandomized on 11 June 2010 to control for position effects, therefore making each trap treatment, block, and date a replicate. Beetles were collected on 11 and 25 June 2010 and sorted to species and sexed. Traps captured only cerambycid beetles in significant numbers.

Beetles were identified using the keys of Gressitt (1951), Gressitt et al. (1970), and Hua et al. (2009). Voucher specimens have been deposited in the museum collection of Guangxi University, Guangxi, China.

We compared the utility of using pheromone lures as probes for assessing the species diversity of cerambycid beetles in terms of the total numbers of species and individuals captured per treatment. Differences

Table 1. Number of cerambycid beetle species and individuals attracted to pheromone compounds and controls

Treatment	Treatment code	No. of species	No. of individuals
(2R^*,3R^*)-2,3-hexanediol	1	10	347
(2R^*,3S^*)-2,3-hexanediol	2	19	99
3-hydroxyhexan-2-one	3	22	120
(2R^*,3R^*)-2,3-octanediol	4	18	187
(2R^*,3S^*)-2,3-octanediol	5	21	319
3-hydroxyoctan-2-one	6	12	28
3-hydroxydecan-2-one	7	12	25
2-(undecyloxy)-ethanol	8	20	303
Fuscumol	9	12	24
Fuscumol acetate	10	7	24
Ethanol control	11	11	37
Unbaited control	12	9	13
Totals		71[a]	1,526

[a] Total is less than the sum of the column because many species were caught in more than one treatment.

between treatment means (number of species or number of individuals per treatment and replicate; sexes combined) were tested using the nonparametric Friedman's test (PROC FREQ, option CMH; SAS Institute 2001). Differences between pairs of means were tested with the REGWQ means-separation test, which controls for maximum experiment-wise error rates (PROC GLM, SAS Institute 2001). This analysis was conducted separately for the dominant subfamilies (Cerambycinae and Lamiinae) to assess taxonomic patterns of attraction to individual treatments. The same statistical approach was used to test treatment effects for mean numbers of specimens for individual species, including only replicates with a threshold number of specimens (threshold 4–8 specimens per replicate, depending on the total number captured) so as to exclude periods of low beetle activity, for example, due to inclement weather.

We also tested for deviations from a 1:1 sex ratio of each species captured using the χ^2 goodness-of-fit test. However, because we have no information on sex ratios within the local populations, biased sex ratios of captured beetles should not be taken as evidence that the sexes differed in their attraction to trap baits.

Results

During the 4-wk trapping period, 1,526 cerambycid beetles of 71 species were captured (Table 1), of which 92% ($N = 1{,}404$) were represented by the top 14 species (Table 2). Most of the species were in the subfamilies Cerambycinae and Lamiinae, with only two species each in the Prioninae and Lepturinae. The greatest numbers of cerambycine species were caught in traps baited with 3-hydroxyhexan-2-one (Fig. 1A; significantly different from controls). Traps baited with (2R^*,3R^*)-2,3-hexanediol attracted much greater numbers of cerambycine individuals than any other treatment (Fig. 1B), mostly due to the abundance of *R. horsfieldi* (White) (see further text). Other compounds that were significantly attractive to cerambycines (relative to controls) were the (2R^*,3R^*)- and (2R^*,3S^*)-octanediols and 3-hydroxyhexan-2-one (Fig. 1B). In contrast, the greatest numbers of lamiine species and individuals were caught by traps baited with 2-(undecyloxy)ethanol (Fig. 1A and B).

All treatments, with the exception of 3-hydroxyoctan-2-one, 3-hydroxydecan-2-one, fuscumol, and fuscumol acetate, attracted at least one species in numbers significantly greater than controls (Table 2). As mentioned earlier, the cerambycine *R. horsfieldi* (tribe Clytini) was caught in the largest numbers overall (532 individuals), being strongly attracted to (2R^*,3R^*)-2,3-hexanediol, followed by (2R^*,3R^*)-2,3-octanediol (Fig. 2; Table 2). The sex ratio was significantly female biased for both treatments (Fig. 2). The congener *Rhaphuma laosica* Gressitt & Rondon was significantly attracted to the six-carbon diastereomer (2R^*,3S^*)-2,3-hexanediol, with 34 of the 35 individuals (18 females; 16 males) captured by traps baited with that chemical (mean 8.5 ± 2.8; means for other treatments <0.2 beetles; Table 2).

Four other cerambycine species, all within the tribe Clytini, were attracted only to 3-hydroxyhexan-2-one (Table 2), including *Xylotrechus atronotatus draconiceps* Gressitt (Fig. 3A), *Demonax literatus literatus* Gahan (Fig. 3B), and their congeners *Xylotrechus incurvatus* (Chevrolat) (mean 7.0 ± 2.4; means for other treatments <0.9) and *Demonax gracilestriatus* Gressitt & Rondon (mean 1.7 ± 0.7; means for other treatments $= 0$). Sex ratios for *X. a. draconiceps* and *D. l. literatus* were not significantly different from 1:1 ($P > 0.05$), but female biased for *X. incurvatus* (2.5:1 F:M; $\chi^2 = 10.0$, $P < 0.01$), and male biased for *D. gracilestriatus* (1:5.5 F:M; $\chi^2 = 9.0$, $P < 0.01$).

Demonax theresae Pic was significantly attracted to (2R^*,3S^*)-2,3-octanediol (mean 9.6 ± 2.0, means for other treatments <0.9; Table 2) with equal sex ratios, whereas its congener *Demonax ordinatus* Pascoe was significantly attracted to (2R^*,3R^*)-2,3-octanediol (mean 4.9 ± 1.3, means for other treatments <0.2; Table 2) with a significant male bias (1:2 F:M; $\chi^2 = 4.33$, $P < 0.05$).

Five lamiine species in the tribe Monochamini were significantly and specifically attracted only to traps baited with 2-(undecyloxy)ethanol (Table 2), including *Acalolepta formosana* (Breuning) (mean 1.3 ± 0.6; means for other treatments <0.4), *Monochamus bimaculatus* (Gahan) (mean 1.0 ± 0.4; means for other treatments <0.2), *Pharsalia subgemmata* (Thomson) (mean 26.9 ± 4.4; means for other treatments <2.2), *Pseudomacrochenus antennatus* (Gahan) (mean 1.50 ± 0.86; means for other treatments <0.4), and *Xenohammus bimaculatus* Schwarzer (mean 3.88 ± 0.91; means for other treatments ≤ 1.0). Sex ratios were significantly female biased for *P. subgemmata* (2:1 F:M; $\chi^2 = 23.5$, $P < 0.001$), significantly male biased for *P. antennatus* and *X. bimaculatus* (1:5 F:M; $\chi^2 = 5.33$, $P < 0.05$; 1:2.6 F:M; $\chi^2 = 7.11$, $P < 0.01$, respectively), but not significantly different from 1:1 for *A. formosana* and *M. bimaculatus* ($P > 0.05$).

Megopsis costipennis White was the single species in the subfamily Prioninae to show a significant treatment effect, with only adult males being strongly at-

Table 2. Numbers of cerambycid beetles captured by traps ($n = 8$ replicates per treatment) in the Bulong Nature Reserve, Yunnan, China, and treatments that had statistically significant means (i.e., significant overall Friedman's Q, and treatment mean significantly greater than mean for control; REGWQ means separation test, $P < 0.05$)

Subfamily and tribe	Genus and species	No.	Significant treatment (Friedman's Q)
Cerambycinae			
Callichromini	*Polyzonas prasinus* (White)	3	–
Cleomenini	*Cleomenes nigricollis* Fairmaire	1	–
Clytini	*Demonax alboantennatus* Gressitt & Rondon	2	–
	Demonax gracilestriatus Gressitt & Rondon	13	3 ($Q_{11,48} = 46.9, P < 0.0001$)
	Demonax literatus literatus Gahan	14	3 ($Q_{11,60} = 18.6, P < 0.05$)
	Demonax ordinatus Pascoe	42	4 ($Q_{11,96} = 73.4, P < 0.001$)
	Demonax theresae Pic	94	5 ($Q_{11,96} = 66.9, P < 0.001$)
	Clytocera montensi Gressitt & Rondon	1	–
	Perissus mimicus Gressitt & Rondon	3	–
	Grammographus notabilus cuneatus (Fairmaire)	6	–
	Perissus griseus Gressitt	2	–
	Rhaphuma anongi Gressitt & Rondon	3	–
	Rhaphuma eleodina Gressitt & Rondon	1	–
	Rhaphuma horsfieldi (White)	542	1, 4 ($Q_{11,84} = 62.6, P < 0.001$)
	Rhaphuma laosica Gressitt & Rondon	35	2 ($Q_{11,48} = 40.3, P < 0.001$)
	Xylotrechus atronotatus draconiceps Gressitt	15	3 ($Q_{11,48} = 40.3, P < 0.001$)
	Xylotrechus buqueti (Castelnau & Gory)	4	–
	Xylotrechus formosanus Scharzer	2	–
	Xylotrechus incurvatus (Chevrolat)	58	3 ($Q_{11,84} = 69.1, P < 0.001$)
	Xylotrechus unicarinatus Pic	6	–
Thraniini	*Thranius granulatus* Pic	1	–
Lamiinae			
Agniini	*Acalolepta basiplagiata* (Breuning)	1	–
	Acalolepta formosana (Breuning)	17	8 ($Q_{11,60} = 38.1, P < 0.001$)
	Epepeotes uncinatus salvazai Pic	1	–
Gleneini	*Glenia diverselineata intermedia* Breuning	2	–
Gnomini	*Coptops annulipes* Gahan	1	–
	Mesosa rupta (Pascoe)	8	–
	Mesosa subtenuefasciata Breuning	8	–
Lamiini	*Blepephaeus stigmosus* Gahan	1	–
	Blepephaeus variegatus Gressitt	2	–
	Monochamus bimaculatus Gahan	13	8 ($Q_{11,84} = 62.6, P < 0.001$)
	Paraleprodera carolina (Fairmaire)	2	–
	Pharsalia subgemmata (Thomson)	306	8 ($Q_{11,96} = 41.1, P < 0.001$)
	Pseudomacrochenus antennatus (Gahan)	19	8 ($Q_{11,72} = 40.3, P < 0.001$)
	Pseudonemophas versteegi (Ritsema)	1	–
	Xenohammus bimaculatus Schwarzer	55	8 ($Q_{11,96} = 38.6, P < 0.001$)
Niphonini	*Alidus biplagiatus* Gahan	6	–
	Pterolophia chekiangensis Gressitt	3	–
	Pterolophia kaleea (Bates)	1	–
	Sthenias gracilicornis (Gressitt)	4	–
Rhodopinini	*Parectatosia valida* Breuning	4	–
Prioninae			
Megopidini	*Megopis costipennis* White	181	5 ($Q_{11,96} = 74.6, P < 0.001$)

Treatment codes as in Table 1. Data are omitted for low numbers of specimens (1–3) of species that could not be fully identified, including 4 cerambycine, 12 lamiine, 2 lepturine, and 1 prionine species.

tracted to (2R*,3S*)-2,3-octanediol (mean 21.9 ± 4.5 males; means for other treatments <0.7).

Discussion

Traps baited with 10 known cerambycid pheromones were effective in attracting a large number of cerambycid species. Collectively, 55 species were captured by traps baited with five compounds, (2R*,3S*)-2,3-hexanediol, 3-hydroxyhexan-2-one, (2R*,3R*)-2,3-octanediol, (2R*,3S*)-2,3-octanediol, and 2-(undecyloxy)ethanol, accounting for >77% of the total number of species. Multiple cerambycine species within the genera *Demonax*, *Rhaphuma*, and *Xylotrechus* were attracted to compounds with diol or hydroxyketone structural motifs, whereas several lamiine species were attracted to the hydroxyether compound 2-(undecyloxy)ethanol (Table 2). Treatment effects were statistically significant for 14 species, suggesting that the compounds to which they were attracted are likely pheromone components. For 13 of these species, all in the subfamilies Cerambycinae and Lamiinae, beetles of both sexes were attracted, suggesting that the compounds are probably male-produced aggregation pheromones attractive to both sexes, consistent with volatile pheromones from many species in these subfamilies that have been identified to date (Hanks and Millar 2013 and references therein).

For the 14th species, *M. costipennis* in the subfamily Prioninae, only males were attracted to (2R*,3S*)-2,3-octanediol, suggesting that this compound is a fe-

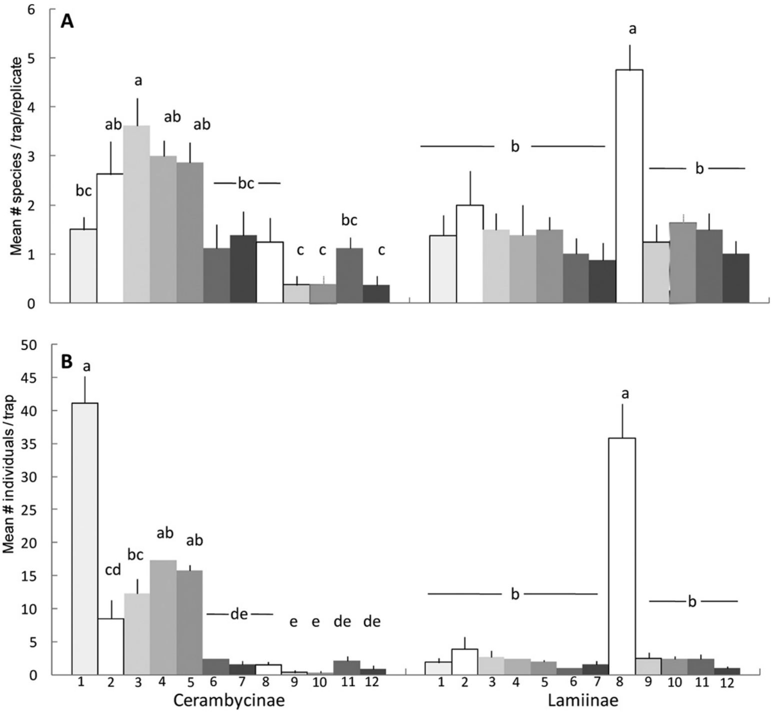

Fig. 1. Mean (±1 SE) number of (A) cerambycid species and (B) individuals of two subfamilies captured by traps (n = 8) baited with synthetic pheromones in the Bulong Nature Reserve, Yunnan, China. Treatment codes as in Table 1. Means significantly different (overall analysis for cerambycines, sexes combined: (A) Friedman's $Q_{11,96} = 50.6, P < 0.001$; (B) $Q_{11,96} = 73.1, P < 0.001$; Lamiinae: (A) $Q_{11,96} = 25.6, P < 0.01$; (B) $Q_{11,96} = 29.4, P < 0.01$. Means within subfamilies with the different letters are significantly different (REGWQ means separation test, $P < 0.05$).

male-produced sex pheromone rather than an aggregation pheromone. This finding again fits the emerging pattern of pheromone use within this subfamily: a female-produced sex pheromone (3,5-dimethyldodecanoic acid) has been identified from the prionine species *Prionus californicus* Motschulsky (Rodstein et al. 2009), and the same compound also is highly attractive to only males of a number of congeners, and thus a likely sex pheromone for these species (Barbour et al. 2011). In a different prionine tribe (Meroscelisini), female *Tragosoma depsarium* sp. nov. Laplante produce (2*R*,3*R*)-2,3-hexanediol, a shorter-chain homolog of the *M. costipennis* attractant, from specialized pores on the prothorax (Ray et al. 2012).

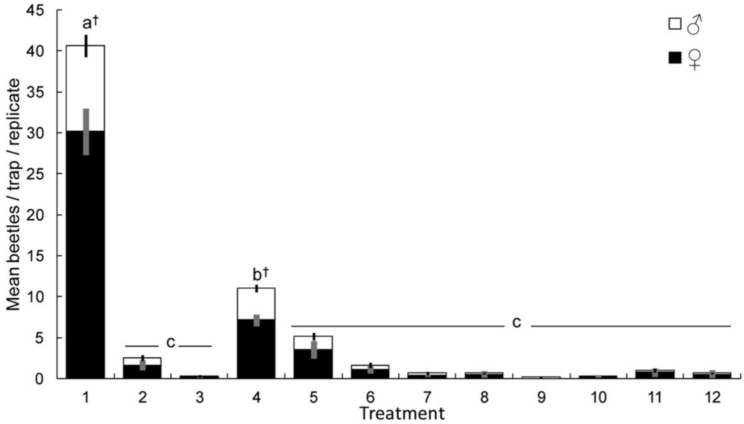

Fig. 2. Mean (±1 SE) number of adult *Rhaphuma horsfieldi* captured in panel traps baited with synthetic pheromones in the Bulong Nature Reserve, Yunnan, China. Treatment codes as in Table 1. Means with the different letters (sexes combined) are significantly different (REGWQ means separation test, $P < 0.05$). † denotes a significant departure from 1:1 F:M sex ratio (2.9:1 F:M for the hexanediol; $\chi^2 = 75.8$, $P < 0.001$; 1:1.9 F:M for the octanediol; $\chi^2 = 10.1$, $P < 0.01$).

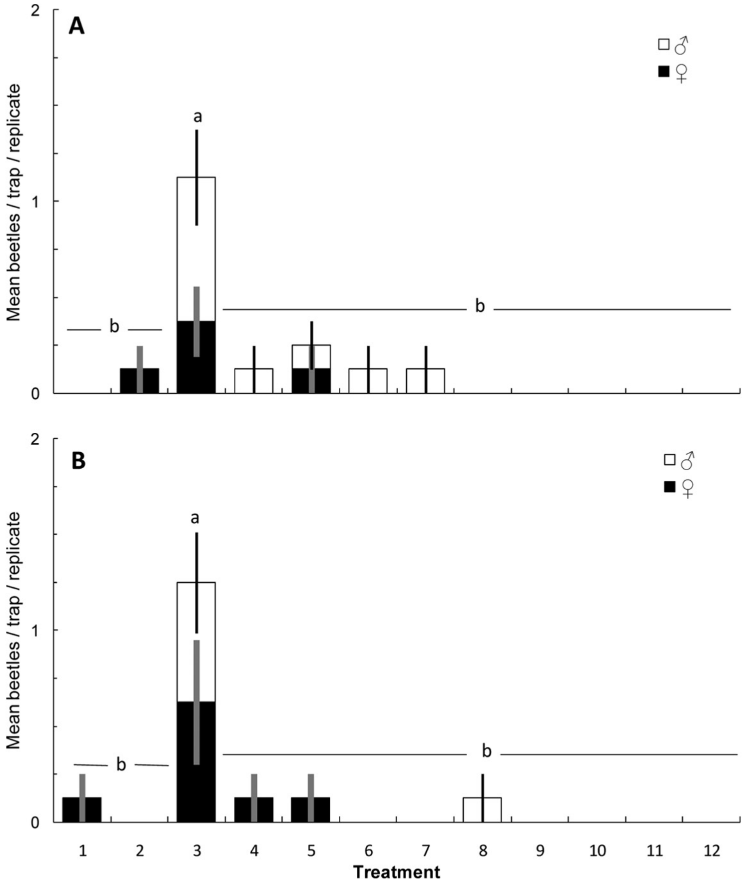

Fig. 3. Mean (±1 SE) number of adult (A) *Xylotrechus atronotatus draconiceps*, and (B) *Demonax literatus literatus* captured in panel traps baited with synthetic pheromones in the Bulong Nature Reserve, Yunnan, China. Treatment codes as in Table 1. Means within subfamilies with different letters (sexes combined) are significantly different (REGWQ means separation test, $P < 0.05$).

Males of two other *Tragosoma* species, *Tragosoma pilosicorne* Casey and *Tragosoma depsarium harrisi* Leconte, are attracted to the diastereomer, (2*S*,3*R*)-2,3-hexanediol, strongly suggesting that this compound is a female-produced sex pheromone for these species. These diols, or stereoisomers or homologs thereof, have been identified or strongly implicated as being male-produced aggregation pheromones for a number of species in the subfamily Cerambycinae, including *R. horsfieldi*, *R. laosica*, *D. theresae*, and *D. ordinatus* in the current study. It is remarkable that the same or very similar compounds are serving as male-produced aggregation pheromones in one subfamily, and female-produced sex pheromones in another.

The compound 3-hydroxyhexan-2-one is a common pheromone component or attractant for numerous species in the subfamily Cerambycinae in North America (Hanks et al. 2007, Graham and Poland 2012, Hanks and Millar 2013). In the current study carried out in China, this compound attracted beetles of more species than any of the other compounds tested, providing further evidence that it is a highly conserved pheromone component among cerambycids. The 2,3-hexanediols and 2,3-octanediols also attracted significant numbers of cerambycine species and individuals. In fact, (2*S*,3*S*)-2,3-octanediol was a component of the first pheromone blend ever reported for a cerambycid species, being produced by males of the Asian species *Xylotrechus pyrrhoderus* Bates, along with the related (*S*)-2-hydroxyoctan-3-one (Sakai et al. 1984). Eight-carbon diols and hydroxyketones also are produced by males of the congeneric *Xylotrechus chinensis* Chevrolat in Japan (Iwabuchi et al. 1987) and *Xylotrechus quadripes* Chevrolat in India (Hall et al. 2006a).

Although fuscumol and fuscumol acetate serve as pheromone components or attractants for several species in the subfamilies Lamiinae and Spondylidinae of North America, South America, and Europe (Silk et al. 2007, Fonseca et al. 2010, Sweeney et al. 2010, Mitchell et al. 2011, Hanks and Millar 2013, Hughes et al. 2013), neither compound attracted significant numbers of any species during the current study in southwest China. In contrast, traps baited with 2-(undecyloxy)ethanol, which to date had only been reported as a pheromone component for lamiine species in the genus *Monochamus* (Pajares et al. 2010, Teale et al.

2011, Allison et al. 2012, Fierke et al. 2012, Macias-Samano et al. 2012, Pajares et al. 2013), attracted one *Monochamus* species and four lamiine species in different genera. This finding is in marked contrast to studies conducted in North America and Europe, where extensive field trials using 2-(undecyloxy)ethanol as a lure have not attracted any lamiine species in genera other than *Monochamus.* Thus, in southern Asia at least, 2-(undecyloxy)ethanol may be a relatively common pheromone component for species within the subfamily Lamiinae. The structural similarities between 2-(undecyloxy)ethanol and 4-(heptyloxy)butan-1-ol and 4-(heptyloxy)butanal, the compounds reported as pheromone components of *A. glabripennis,* the Asian longhorned beetle (Zhang et al. 2002), and 2-(heptyloxybutyloxy)ethanol, a pheromone component of *Monochamus leuconotus* Leconte (Hall et al. 2006b), suggest that other analogs of these structures might be used as pheromones by related species. However, no beetles have been caught in traps baited with four such analogs in field trials conducted in China and North America in recent years (J.D.W., unpublished data).

We have yet to confirm whether the cerambycid species captured in bioassays in China actually produce the compounds to which they were attracted. It is possible that a few of the responses may actually be kairomonal responses to the pheromones of species that compete for the same larval hosts. This phenomenon had been previously noted for two cerambycid species in the genus *Phymatodes* that are attracted to 3-hydroxyhexan-2-one, even though their own male-produced pheromones comprise only (*R*)-2-methylbutan-1-ol (Hanks et al. 2007, Hanks and Millar 2013). Efforts to collect pheromones from the Chinese species *R. horsfieldi* and *P. subgemmata* were not successful, with no pheromone components detected in volatiles collected from beetles of either sex, in both 2011 and 2012.

Overall, it is important to understand the patterns of pheromone use by closely related species that may share pheromone components, and that may be sympatric, be synchronic, and share larval hosts, so that there is potential for cross-attraction. Clearly, mechanisms must exist for limiting unproductive attraction between heterospecifics. Recent results from testing pheromone lures in North America have revealed one such mechanism: antagonism or inhibition of attraction of species to their primary pheromone component when pheromone components of sympatric species are added to a multicomponent lure (Hanks and Millar 2013). Because of the complexity of insect–host plant interactions, especially in the tropics (Erwin 1982, Tavakilian et al. 1997), it also is likely that host plant chemicals may play a role in limiting cross-attraction between species that share pheromone components, but which colonize different types of hosts.

In summary, our study provides further support for the hypothesis that many pheromone components are highly conserved within the Cerambycidae, with a small number of known pheromone components resulting in widespread attraction of many species. To our knowledge, the current study is the first large-scale screening study of cerambycid pheromones in China, and the results are consistent with those from similar studies conducted in North America (Hanks and Millar 2013) and eastern Europe (Imrei et al. 2013). In addition to the strong attraction of 14 species, the lesser attraction of numerous other species provides strong leads to be followed up, to fully identify the pheromones of the responding species. Furthermore, it must be emphasized that only individual compounds were tested in this study, and that tests with blends of compounds would almost certainly result in greatly increased attraction of at least some of these species (for examples, see Hanks and Millar 2013). Traps baited with six- and eight-carbon diols captured a diversity of cerambycine species ($\approx$25), as well as the prionine species *M. costipennis,* whereas 2-(undecyloxy)ethanol was shown to be an attractant for species in an additional five lamiine genera. In a practical context, the results have provided valuable baseline information on the biodiversity of native cerambycid species in an Asian rain forest. The identification of attractants and likely pheromones for a number of Asian species also will be useful to regulatory agencies in other areas of the world should any of these species be introduced and prove to be invasive.

Acknowledgments

We gratefully acknowledge financial support to J.D.W. from the National Natural Sciences Foundation of China (grant 21050110424 and 21150110575), the Chinese Academy of Sciences Fellowships for Young International Scientists (grant 2010Y1JB1), and the United States National Science Foundation (award no. OISE-0904100), and to J.G.M. and L.M.H. from the United States Department of Agriculture–Animal and Plant Health Inspection Service (agreements 09-8100-1422-CA, 10-8130-1422-CA, and 11-8130-1422-CA). Field site funding was provided by the Consultative Group on International Agricultural Research (CGIAR) Research Program 6: Forests, Trees and Agroforestry sponsored by the Food and Agriculture Organization of the United Nations, the International Fund for Agricultural Development, the United Nations Development Program, and the World Bank. We also thank Lai Han, Mei Long, and Noah Elbot for assistance with field trapping studies.

References Cited

Allison, J. D., C. W. Johnson, J. R. Meeker, B. L. Strom, and S. M. Butler. 2011. Effect of aerosol surface lubricants on the abundance and richness of selected forest insects captured in multiple-funnel and panel traps. J. Econ. Entomol. 104: 1258–1264.

Allison, J. D., J. L. McKenna, J. G. Millar, J. S. McElfresh, R. F. Mitchell, and L. M. Hanks. 2012. Response of the woodborers *Monochamus carolinensis* and *Monochamus titillator* (Coleoptera: Cerambycidae) to known cerambycid pheromones in the presence and absence of the host plant volatile α-pinene. Environ. Entomol. 41: 1587–1596.

Barbour, J. D., J. G. Millar, J. Rodstein, A. M. Ray, D. G. Alston, M. Rejzek, J. D. Dutcher, and L. M. Hanks. 2011. Synthetic 3,5-dimethyldodecanoic acid serves as a general attractant for multiple species of *Prionus* (Coleoptera: Cerambycidae). Ann. Entomol. Soc. Am. 104: 588–593.

Brockerhoff, E. G., A. M. Liebhold, and H. Jactel. 2006. The ecology of forest insect invasions and advances in their management. Can. J. For. Res. 36: 263–268.

Duffy, E.A.J. 1953. A monograph of the immature stages of British and imported timber beetles (Cerambycidae). British Museum (National History), London, United Kingdom.

Duffy, E.A.J. 1968. A monograph of the immature stages of oriental timber beetles (Cerambycidae). British Museum (National History), London, United Kingdom.

Erwin, T. L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. Coleopterists Bull. 36: 74–75.

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.

Fonseca, M. G., D. M. Vidal, and P.H.G. Zarbin. 2010. Male-produced sex pheromone of the cerambycid beetle *Hedypathes betulinus:* chemical identification and biological activity. J. Chem. Ecol. 36: 1132–1139.

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.

Graham, E. E., and T. M. Poland. 2012. Efficacy of Fluon conditioning for capturing cerambycid beetles in different trap designs and persistence on panel traps over time. J. Econ. Entomol. 105: 395–401.

Graham, E. E., T. M. Poland, D. G. McCullough, and J. G. Millar. 2012. A comparison of trap type and height for capturing cerambycid beetles (Coleoptera). J. Econ. Entomol. 105: 837–846.

Gressitt, J. L. 1951. Longicorn beetles of China. Longicornia 2: 1–667.

Gressitt, J. L., J. A. Rondon, and S. von Bruening. 1970. Cerambycid beetles of Laos. Pac. Insects Monogr. 24: 1–651.

Haack, R. A. 2006. Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions. Can. J. For. Res. 36: 269–288.

Haack, R. A., F. Hérard, J. Sun, and J. J. Turgeon. 2010. Managing invasive populations of Asian longhorned beetle and citrus longhorned beetle: a worldwide perspective. Annu. Rev. Entomol. 55: 521–546.

Hall, D. R., A. Cork, S. J. Phythian, S. Chittamuru, B. K. Jayarama, M. G. Venkatesha, K. Sreedharan, P. K. Vinod Kumar, H. G. Seetharama, and R. Naidu. 2006a. Identification of components of male-produced pheromone of coffee white stemborer, *Xylotrechus quadripes.* J. Chem. Ecol. 32: 195–219.

Hall, D. R., D. Kutywayo, C. Chanika, S. Nyirenda, and G. Oduor. 2006b. Chemistry of the African coffee stemborer, *Monochamus leuconotus:* but where's the ecology?, p. 306. In Abstracts, 22nd Meeting of the International Society of Chemical Ecology, 2006, Barcelona, Spain.

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., 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.

Hua L. Z., N. Hajime, G. A. Samuelson, and S. W. Lingafelter. 2009. Iconography of Chinese longicorn beetles. Sun Yat-Sen University Press, Guangzhou, China.

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: 1–6.

Imrei, Z., J. G. Millar, G. Janik, and M. Toth. 2013. Field screening of known pheromone components of longhorned beetles in the subfamily Cerambycinae (Coleoptera: Cerambycidae) in Hungary. Z. Naturforsch 68c: 236–242.

Iwabuchi, K., J. Takahashi, and T. Sakai. 1987. Occurrence of 2,3-octanediol and 2-hydroxy-3-octanone, possible male sex pheromone in *Xylotrechus chinensis* Chevrolat (Coleoptera: Cerambycidae). Appl. Entomol. Zool. 22: 110–111.

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.

Linsley, E. G. 1961. The Cerambycidae of North America: part I. Introduction. Univ. Calif. Publ. Entomol 18: 1–97.

Linsley, E. G., and J. A. Chemsak. 1997. The Cerambycidae of North America, part VIII: bibliography, index, and host plant index. Univ. Calif. Publ. Entomol. 117: 1–534.

Macias-Samano, J. E., D. Wakerchuk, J. G. Millar, and L. M. Hanks. 2012. 2-Undecyloxy-1-ethanol in combination with other semiochemicals attracts three *Monochamus* species (Coleoptera: Cerambycidae) in British Columbia, Canada. Can. Entomol. 144: 821–825.

Millar, J. G., L. M. Hanks, J. A. Moreira, J. D. Barbour, and E. S. Lacey. 2009. Pheromone chemistry of cerambycid beetles, pp. 52–79. *In* K. Nakamuta and J. G. Millar (eds.), Chemical Ecology of Wood-Boring Insects. Forestry and Forest Products Research Institute, Ibaraki, Japan.

Mitchell, R. F., E. E. Graham, J. C. 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.

Pajares, J. A., G. Alvarez, F. Ibeas, D. Gallego, D. R. Hall, and D. I. Farman. 2010. Identification and field activity of a male-produced aggregation pheromone in the pine sawyer beetle, *Monochamus galloprovincialis.* J. Chem. Ecol. 36: 570–583.

Pajares, J. A., G. Alvarez, D. R. Hall, P. Douglas, F. Centeno, N. Ibarra, M. Schroeder, S. A. Teale, Z. Wang, S. Yan, J. G. Millar, and L. M. Hanks. 2013. 2-(Undecyloxy)-ethanol is a major component of the male-produced aggregation pheromone of *Monochamus sutor.* Entomol. Exp. Appl. 149: 118–127.

Ray, A. M., J. D. Barbour, J. S. McElfresh, J. A. Moreira, I. P. Swift, I. M. Wright, A. Žunic, R. F. Mitchell, E. E. Graham, R. L. Alten, J. G. Millar, and L. M. Hanks. 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: 1–8.

Ray, A. M., A. Žunič, 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.

Rodstein, J., J. S. McElfresh, J. D. Barbour, A. M. Ray, L. M. Hanks, and J. G. Millar. 2009. Identification and synthesis of a female-produced sex pheromone for the cerambycid beetle *Prionus californicus.* J. Chem. Ecol. 35: 590–600.

SAS Institute. 2001. SAS/STAT user's guide for personal computers, release 8.01. SAS Institute, Cary, NC.

Sakai, T., Y. Nakagawa, J. Takahashi, K. Iwabuchi, and K. Ishii. 1984. Isolation and identification of the male sex pheromone of the grape borer *Xylotrechus pyrrhoderus* Bates (Coleoptera: Cerambycidae). Chem. Lett. 1984: 263–264.

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: 679–701.

Sweeney, J., P. J. Silk, J. M. Gutowski, J. Wu, and M. A. Lemay. 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.

Tavakilian, G., A. Berkov, B. Meurer-Grimes, and S. Mori. 1997. Neotropical tree species and their faunas of xylophagous longicorns (Coleoptera: Cerambycidae) in French Guiana. Botanical Rev. 63: 303–355.

Teale, S. A., J. D. Wickham, F. Zhang, J. Su, Y. Chen, W. Xiao, L. M. Hanks, and J. G. Millar. 2011. A male-produced aggregation pheromone of *Monochamus alternatus* (Coleoptera: Cerambycidae), a major vector of pine wood nematode. J. Econ. Entomol. 104: 1592–1598.

Wang, Z. J., C. Carpenter, and S. S. Young. 2000. Bird distribution and conservation in the Ailao mountains, Yunnan, China. Biol. Conserv. 92: 45–57.

Xu, J., L. Lebel, and J. Sturgeon. 2009. Functional links between biodiversity, livelihoods, and culture in a Hani Swidden landscape in southwest China. Ecol. Soc. 14: 20–37.

Zhang, A., J. E. Oliver, J. R. Aldrich, B. Wang, and V. C. Mastro. 2002. Stimulatory beetle volatiles for the Asian longhorned beetle, *Anoplophora glabripennis* (Motschulsky). Z. Naturforsch. 57: 553–558.

Received 20 July 2013; accepted 5 November 2013.