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Cerambycid Pheromones Attract Predators *Temnoscheila virescens* (Coleoptera: Trogossitidae), *Chariessa pilosa* (Coleoptera: Cleridae), and *Apiomerus crassipes* (Hemiptera: Reduviidae)

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Abstract

In 2011–2013, we determined the interactive effects of the cerambycid pheromones racemic *syn*-2,3-hexanediol, racemic 3-hydroxyhexan-2-one, and racemic 3-hydroxyoctan-2-one on trap catches of predators associated with bark and woodboring beetles in north Georgia and South Carolina. *Temnoscheila virescens* (F.) (Coleoptera: Trogossitidae) was attracted to traps baited with 3-hydroxyhexan-2-one; ethanol enhanced attraction. Traps baited with *syn*-2,3-hexanediol attracted *Chariessa pilosa* (Forster) (Coleoptera: Cleridae); attraction was interrupted by 3-hydroxyhexan-2-one. An assassin bug *Apiomerus crassipes* (F.) (Hemiptera: Reduviidae) was attracted to traps baited with 3-hydroxyhexan-2-one and/or 3-hydroxyoctan-2-one. Ethanol had no effect on trap catches of *C. pilosa* and *A. crassipes*. We compared response profiles of these predators to those of longhorn beetles captured in these same studies to provide insights on possible ecological interactions between these species.

Key words: predator, Cleridae, Trogossitidae, Reduviidae, kairomone

Longhorn beetles (Coleoptera: Cerambycidae) play critical roles in the breakdown and decomposition of dead, dying or downed trees, shrubs, and branches (Wang 2017). Activities by woodboring cerambycids help facilitate nutrient cycling, reduce fire fuel loads, favor understory growth, and enhance wildlife activities. Except for a few pest species, the population biologies of most cerambycids are relatively unknown (Nielsen 1981, Evans et al. 2007, Kenis and Hilszczanski 2007, Paine 2017).

Woodpeckers (Picidae) and parasitoids (Hymenoptera and Diptera) are broadly known as biological control agents of bark and woodboring beetles (Solomon 1995, Kenis and Hilszczanski 2007, Paine 2017). However, Solomon (1995) noted several species of Cleridae and Trogossitidae (Coleoptera) as possible predators for several species of cerambycids found in broadleaf trees. As with Cerambycidae, bark and ambrosia beetles (Coleoptera: Curculionidae) commonly occur in subcortical habitats (Raffa et al. 2015). Clerids and trogossitids are widely recognized as general predators of bark and ambrosia beetles (Kenis et al. 2007, Wegensteiner et al. 2015). Given that larval cerambycids may be present at the same time as bark and ambrosia beetle larvae, it is possible that clerid and trogossitid predators may also prey on larval cerambycids. However, there is very little documented evidence in the literature of clerid or trogossitid predation on cerambycids.

Studies on the chemical ecology of species associated with bark and woodboring beetles can provide insights into their respective ecological roles. Predators eavesdrop on the pheromone channels of bark beetles, responding to their pheromones as kairomones to locate their bark beetle prey (Kenis et al. 2007, Raffa et al. 2015, Wegensteiner et al. 2015). Consequently, predators attracted to the pheromones used by cerambycid species could increase the likelihood of predator-prey interactions between them, given that they all occupy sub-cortical habitats. In Europe, pheromones of *Plagionotus detritus* (L.) (Coleoptera: Cerambycidae) attract the predator *Clerus mutilatus* F. (Coleoptera: Cleridae) (Imrei et al. 2021). Similarly in central Europe, traps baited with a complex blend of six cerambycid pheromones were attractive to *C.*

mutilatus and the longhorn beetles *Phymatodes testaceus* (L.) (Coleoptera: Cerambycidae), *Leiopus nebulosus* (L.) (Coleoptera: Cerambycidae) and *Pyrrhidium sanguineum* (L.) (Coleoptera: Cerambycidae) (Imrei et al. 2022). In the United States, Miller and Crowe (2020) found that sulcatol, a pheromone used by ambrosia and longhorn beetles, attracted four species of predators along with *Monarthrum mali* (Fitch) (Coleoptera: Curculionidae) and *Leptostylus asperatus* (Haldeman) (Coleoptera: Cerambycidae). Miller et al. (2015, 2022) noted attraction of the predators *Chariessa pilosa* (Forster) (Coleoptera: Cleridae), *Enoclerus ichneumonus* (F.) (Coleoptera: Cleridae), *Madoniella dislocata* (Say) (Coleoptera: Cleridae), *Temnoscheila virescens* (F.) (Coleoptera: Trogossitidae) and *Apiomerus crassipes* (F.) (Hemiptera: Reduviidae) to traps baited with the cerambycid pheromones *anti*-2,3-hexanediol, *syn*-2,3-hexanediol and 3-hydroxyhexan-2-one in southern United States.

Seven trapping experiments were conducted in 2011–2013 to determine the interactive effects of the cerambycid pheromones *syn*-2,3-hexanediol, 3-hydroxyhexan-2-one, and 3-hydroxyoctan-2-one on catches of Cerambycidae, Curculionidae and associated predators. Our trapping results have been published for Cerambycidae (Miller et al. 2017) and Curculionidae (Miller and Sweeney 2022). Herein, we report on the lure preferences of predators captured in the seven experiments.

Materials and Methods

Seven trapping experiments were conducted in mature, pine-oak stands in Georgia and South Carolina (Table 1). Experiment 2 was conducted at the Rock Eagle 4-H Center, Putnam Co., GA whereas Experiment 5 was conducted at the Harbison State Forest, Richland Co., SC. All other experiments were conducted on the Oconee National Forest (Greene and Putnam Counties, GA). We baited traps with the following lures: black plastic sealed pouches (5.5 × 30 cm) containing ethanol (release rate (RR) = 0.5 g/d at 23°C); white plastic sealed pouches (10 × 8 cm) containing racemic *syn*-2,3-hexanediol in orange cellulose pads (6.5 × 6.5 cm) (RR = 1.5 mg/d at 20°C); brown plastic sealed pouches (5 × 12 cm) containing racemic 3-hydroxyhexan-2-one in orange cellulose pads (4 × 7 cm) (RR = 20–25 mg/d at 20°C); and brown plastic sealed pouches (5 × 12 cm) containing racemic 3-hydroxyoctan-2-one in orange cellulose pads (4 × 7 cm) (RR = 20–25 mg/d at 20°C). All lures were manufactured by Contech Enterprises (Victoria, BC) with all chemical purities >95%. Release rates were determined by the manufacturer.

The trapping protocols have been published previously in Miller et al. (2017). Seven different experiments were set with lure treatments noted in Table 2. We used a complete randomized block design in each experiment: eight blocks of traps in Experiments 1–3, ten blocks in Experiments 4, 5, and 7, and nine blocks in Experiment 6. In each experiment, lure treatments were randomly assigned to a trap within a block. Lindgren multiple-funnel (10-unit) traps (Synergy Semiochemicals Inc., Delta, BC) were modified as in Miller et al. (2013) to allow lures to hang within the traps. Traps were hung on twine strung between trees. In each experiment, traps were deployed in a curvilinear pattern through a stand with a spacing between traps of 8–12 m; the end of a block was 8–12 m from the next block. Each collection cup contained approximately 150 ml of ethanol-free Splash RV & Marine Antifreeze (Splash Products Inc., St. Paul, MN) (Miller and Duerr 2008). Voucher specimens were deposited in the University of Georgia Collection of Arthropods (UGCA), Athens, GA.

Trap catch data were analyzed with the SYSTAT (ver. 13) and SigmaStat (ver. 3.01) statistical packages (SYSTAT Software Inc., Point Richmond, CA). All analyses were conducted by mixed-model ANOVA with block as a random factor for species with total catch ≥30 in an experiment. As needed to meet assumptions of normality and homoskedasticity (verified by the Shapiro-Wilk and Equal Variance tests, respectively), data were transformed by $\ln(Y + 1)$ (Pepper et al. 1997). In each experiment, data were analyzed by one-way ANOVA (y = lure treatment + block + error) followed by the Holm-Sidak multiple comparison test when $P \leq 0.05$. The Holm-Sidak test controls the experiment-wise error rate at $\alpha = 0.05$ (Glantz 2005). Since Experiment 1 was set as a full-factorial design (3 factors with 2 levels per factor), we further analyzed the data by three-way ANOVA (y = D6 + K6 + K8 + D6 * K6 + D6 * K8 + K6 * K8 + D6 * K6 * K8 + block + error). Similarly, Experiments 4–5 were set as factorial designs (2 factors with 2 levels per factor) and analyzed by two-way ANOVA (y = D6 + K6K8 + D6 * K6K8 + block + error).

Results

We captured substantial numbers of predatory species from six families of Coleoptera and one family of Hemiptera across the seven trapping experiments (Table 3). The three most common species were *T. virescens*, *C. pilosa*, and *A. crassipes*.

Temnoscheila virescens

In Experiment 1, catches of *T. virescens* were significantly enhanced by the addition of K6 to traps (Table 4). Catches were greatest in traps baited with K6 regardless of the addition of D6 and/or K8 (Fig. 1A). Results in Experiment 2 ($F_{5,35} = 23.44$, $P < 0.001$) supported those from Experiment 1. Addition of the K blend to traps baited with either D6 or D6 plus ethanol significantly increased mean catches of

Table 1. Coordinates, dominant tree species, and trapping dates for seven experiments on flight responses of predatory insects to multiple-funnel traps baited with ethanol, *syn*-2,3-hexanediol, 3-hydroxyhexan-2-one and 3-hydroxyoctan-2-one in north Georgia and South Carolina

Exp	Coordinates	Tree species	Trapping dates
1	33.344N, 83.457W	*Quercus alba* L., *Quercus falcata* Michaux, *Liquidambar styraciflua* L., *Pinus echinata* Miller, *Carya tomentosa* Sargent	3 June–12 July 2011
2	33.435N, 83.389W	*Pinus taeda* (L.), *P. echinata*, *L. styraciflua*	24 May–18 July 2012
3	33.744N, 83.282W	*P. taeda*, *Q. alba*, *L. styraciflua*	9 April–29 May 2013
4	33.742N, 83.282W	*P. taeda*, *Q. alba*, *P. echinata*, *L. styraciflua*	16 March–7 May 2012
5	34.086N, 81.116W	*P. taeda*	16 May–10 July 2012
6	33.237N, 83.514W	*Q. alba*, *Q. falcata*, *L. styraciflua L.*, *P. echinata*, *C. tomentosa*	26 April–14 June 2012
7	33.750N, 83.261W	*P. taeda*, *Q. alba*, *P. echinata*	2 August–26 September 2013

Table 2. Lure treatments used in seven randomized-block trapping experiments testing the interactive effects between ethanol, *syn*-2,3-hexanediol, 3-hydroxyhexan-2-one and 3-hydroxyoctan-2-one lures on catches of predatory insects in north Georgia and South Carolina

Exp	Treatments
1	1.**Blank** = No lures
	2.**D6** = *syn*-2,3-hexanediol lure
	3.**K6** = racemic 3-hydroxyhexan-2-one lure
	4.**K8** = racemic 3-hydroxyoctan-2-one lure
	5.**K6K8** = K6 lure + K8 lure
	6.**D6K6** = D6 lure + K6 lure
	7.**D6K8** = D6 lure + K8 lure
	8.**D6K6K8** = D6 lure + K6 lure + K8 lure
2–3	1.**D6** = D6 lure
	2.**K** = K6 lure + K8 lure
	3.**D6K** = D6 lure + K lures
	4.**D6Et** =D6 lure + ethanol UHR lure (**Et**)
	5.**KEt** = K lures + Et lure
	6.**D6KEt** = D6 lure + K lures + Et lure
4–5	1.**Et** = Et lure
	2.**EtD6** = Et lure + D6 lure
	3.**EtK** = Et lure + K6 lure + K8 lure
	4.**EtD6K** = Et lure + D6 lure + K6 lure + K8 lure
6–7	1.**ALL** = Et lure + D6 lure + K6 lure + K8 lure
	2.**ALL – D6** = Et lure + K6 lure + K8 lure
	3.**ALL – K6** = Et lure + D6 lure + K8 lure
	4.**ALL – K8** = Et lure + K6 lure + D6 lure

T. virescens (Fig. 2A). Moreover, mean catches were significantly increased by adding ethanol to traps baited with the K blend, regardless of the presence of D6 (Fig. 2A). Results in Experiment 3 ($F_{5,35}$ = 4.979, P = 0.002) were similar except that ethanol treatment means did not separate from non-ethanol treatment means (Fig. 2B). Adding the K blend plus ethanol to traps baited with D6 significantly increased catches but adding the K blend alone did not affect catches (Fig. 2B).

Similarly, the K blend significantly affected catches of *T. virescens* in Experiments 4–5 (Table 5). In both Georgia and South Carolina, the addition of K blend to ethanol-baited traps significantly increased mean catches of *T. virescens*, regardless of the presence of D6 (Fig. 3A–B). Results in Experiment 6 ($F_{3,24}$ = 68.39, P < 0.001) and Experiment 7 ($F_{3,27}$ = 53.98, P < 0.001) showed that K6 (i.e., racemic 3-hydroxyhexan-2-one) and not K8 was responsible for attraction of *T. virescens* to the K blend in the previous experiments. Catches in traps baited with the 4-component blend were reduced only when K6 was eliminated (Fig. 4A–B).

Chariessa pilosa

In Experiment 1, catches of *C. pilosa* were affected by D6, K6, and their interaction (Table 4). Baiting traps with either D6, K6 or both significantly increased catch whereas K8 had no effect (Fig. 1B). Catches of *C. pilosa* in Experiment 3 were affected by the lure treatments ($F_{5,35}$ = 8.025, P < 0.001); too few beetles were caught in Experiment 2 for analyses (Table 3). Results in Experiment 3 contrasted with those of Experiment 1 in that traps baited with D6 (with or without ethanol) caught more *C. pilosa* than traps baited with the K blend (with or without ethanol) (Fig. 2C). Adding the K blend to traps baited with D6 and ethanol significantly reduced catches.

In Experiments 4–5, catches of *C. pilosa* were affected by D6 and the D6 x K interaction (Table 5). In both Georgia and South Carolina, catches were greater in traps baited with ethanol + D6 than in traps baited solely with ethanol (Fig. 3C–D). As in Experiment 3, adding the K blend to traps baited with D6 + ethanol reduced catches of *C. pilosa*, but the difference was significant in Georgia (Experiment 4) only (Fig. 3C). Catches were affected by lure treatments in Experiment 6 ($F_{3,24}$ = 28.58, P < 0.001); none were caught in Experiment 7 (Table 3). Elimination of K6 enhanced catches of *C. pilosa* in traps baited with the 4-component blend (Fig. 4C).

Apiomerus crassipes

In Experiment 1, catches of *A. crassipes* were affected by K6 and K8 (Table 4). Adding either K6, K8, or both to unbaited traps or traps baited with D6 significantly increased mean catches (Fig. 1C). No *A. crassipes* were caught in Experiment 2 (Table 3) but results in Experiment 3 ($F_{5,35}$ = 13.65, P < 0.001) supported those in Experiment 1 in that adding the K blend to traps baited with D6 significantly increased catches; ethanol had no effect on catches of *A. crassipes* (Fig. 2D). Results of Experiments 4 and 5 confirmed the positive effect of K blend on catch of *A. crassipes* (Table 5) although means were separated in Georgia only (Fig. 3E, F). In Experiment 6, lure treatments had a significant effect on catches of *A. crassipes* ($F_{3,24}$ = 29.92, P < 0.001); none were caught in Experiment 7 (Table 3). Catches were reduced by the elimination of D6, K6, or K8 from the 4-component blend (Fig. 4D). Elimination of K8 reduced catches of *A. crassipes* more than the elimination of D6 or K6.

Other Predator Species

Catches of *Corticotomus depressus* Schaeffer (Coleoptera: Trogossitidae) in Experiment 3 and *Tenebroides* spp. (Coleoptera: Trogossitidae) in Experiments 1–4, 6–7 were unaffected by lure treatments (Table 6).

Associated Species of Coleoptera

A powderpost beetle, *Xylobiops basilaris* (Say) (Bostrichidae), was caught in sufficient numbers for analyses in four of the seven experiments (Table 3). In Experiments 4–5, catches were affected by D6 and the interaction between D6 and K (Table 5). Adding either D6 or the K blend to ethanol-baited traps significantly increased mean catch of *X. basilaris* but when the K blend was added to traps baited with D6+ethanol, mean catches decreased, though not significantly (Fig. 3G–H). Lure treatments had a significant effect on catches in Experiment 6 ($F_{3,24}$ = 17.90, P < 0.001) and in Experiment 7 ($F_{3,27}$ = 61.63, P < 0.001). In both experiments, catches of *X. basilaris* were reduced only by the elimination of D6 from the 4-component blend (Fig. 4E–F).

Lure treatments had no effect on trap catches of *Acmaeodera tubulus* (F.) (Buprestidae) and *Chalcophora virginiensis* (Drury) (Buprestidae) in Experiment 4, *Alaus oculatus* (F.) (Elateridae) in Experiment 1, *Catogenus rufus* (F.) (Passandridae) in Experiments 1, 3, 6–7, *Corticotomus depressus* Schaeffer (Trogossitidae) in Experiment 3, and *Tenebroides* spp (Trogossitidae) in Experiments 1–4, 6–7 (Table 6). Catches of these species appear to be simply random encounters with the traps.

Discussion

Studying the predator-prey relationships of longhorn beetles is challenging, particularly with respect to subcortical predators

Table 3. Total numbers of predatory insects and associates captured in seven trapping experiments conducted in north Georgia and South Carolina (2011–2013)

Order, Family, Species	Exp 1	Exp 2	Exp 3	Exp 4	Exp 5	Exp 6	Exp 7	Total
Coleoptera: Bostrichidae								
Xylobiops basilaris (Say)	–	–	–	1,634	325	460	1,883	4,302
Coleoptera: Buprestidae								
Acmaeodera tubulus (F.)	–	–	–	147	–	–	–	147
Buprestis lineata F.	–	–	–	–	–	5	6	11
Chalcophora virginiensis (Drury)	–	–	–	115	–	–	8	123
Coleoptera: Carabidae								
Coptodera aerata Dejean	–	–	16	–	–	–	–	16
Coleoptera: Cleridae								
Chariessa pilosa (Forster)	331	13	126	92	58	223	–	843
Enoclerus ichneumonus (F.)	–	–	–	28	22	–	–	50
Enoclerus nigripes (Say)	–	–	17	–	–	–	–	17
Thanasimus dubius (F.)	–	10	–	–	–	–	–	10
Coleoptera: Elateridae								
Alaus myops (F.)	60	–	–	13	–	8	–	81
Alaus oculatus (L.)	29	–	–	–	–	12	–	41
Coleoptera: Histeridae								
Platysoma spp.	–	–	17	–	–	–	–	17
Coleoptera: Passandridae								
Catogenus rufus (F.)	35	–	63	–	–	74	53	225
Coleoptera: Tenebrionidae								
Corticeus spp.	–	–	5	–	–	–	–	5
Coleoptera: Trogossitidae								
Corticotomus depressus Schaeffer	–	–	85	–	–	–	–	85
Temnoscheila virescens (F.)	829	414	194	232	365	652	306	2,992
Tenebroides spp.	108	213	220	115	–	343	100	1,099
Hemiptera: Reduviidae								
Apiomerus crassipes (F.)	902	–	142	666	61	1,526	–	3,297
Total number of insects	2,294	650	885	3,042	831	3,303	2,356	13,361

Table 4. ANOVA significance values (***P***) for effects of *syn*-2,3-hexanediol (**D6**), 3-hydroxyhexan-2-one (**K6**), 3-hydroxyoctan-2one (**K8**), and all treatment interactions on trap catches of predatory insect species in Experiment 1. Associated ***F*** values presented in parentheses with df = 1, 49

	P						
Order: Family/Species	**D6**	**K6**	**K8**	**D6 × K6**	**D6 × K8**	**K6 × K8**	**D6 × K6 × K8**
Coleoptera: Cleridae							
Chariessa pilosa	<0.001	<0.001	0.986	<0.001	0.435	0.862	0.249
	(53.24)	(20.95)	(0.001)	(28.58)	(0.619)	(0.030)	(1.359)
Coleoptera: Trogossitidae							
Temnoscheila virescens	0.460	<0.001	0.250	0.703	0.436	0.936	0.123
	(0.555)	(606.2)	(1.354)	(0.147)	(0.618)	(0.006)	(2.462)
Hemiptera: Reduviidae							
Apiomerus crassipes	0.586	<0.001	<0.001	0.303	0.069	<0.001	0.802
	(0.300)	(123.1)	(281.7)	(1.085)	(3.451)	(85.54)	().064)

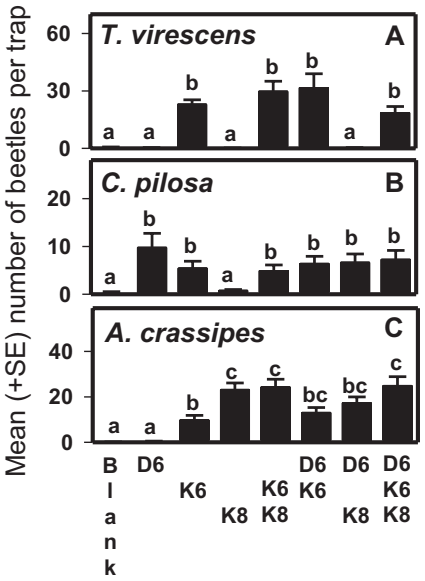

Fig. 1. Effects of *syn*-2,3-hexanediol lure (**D6**), 3-hydroxyhexan-2-one lure (**K6**), and 3-hydroxyoctan-2-one lures (**K8**) on trap catches of *Temnoscheila virescens* (**A**), *Chariessa pilosa* (**B**), and *Apiomerus crassipes* (**C**) in Experiment 1. For each species, means followed by the same letter are not significantly different at $P \leq 0.05$ (Holm-Sidak multiple-comparison test).

and ectoparasites (Nielsen 1981). Much of the development of cerambycids occurs beneath the bark or within woody tissues. Long generation times (one or more years) and unpredictable levels of populations make experimentation problematic. Foraging by woodpeckers on bark and woodboring beetles is obvious, both visually and acoustically. Collections of parasitized cerambycid larvae only require a little time to see what species of parasitoid emerges. Observations of predation on woodboring beetles around adult foraging sites such as flowers or in larval galleries under the bark require considerable time and effort.

Numerous species of clerids and a few species of trogossitids are important predators of bark and ambrosia beetles with adults feeding on adults and larvae feeding on larvae (USDA 1985, Wegensteiner et al. 2015). In southeastern United States, many of these species are attracted to pheromones produced by bark beetles (Allison et al. 2013). Ethanol is broadly attractive to numerous species of ambrosia beetles (Miller and Rabaglia 2009). It is possible that similar relationships exist between predators and cerambycid species, especially with generalist predators that may switch larval preferences based on availability. The effects of *syn*-2,3-hexanediol, 3-hydroxyhexan-2-one, and 3-hydroxyoctan-2-one on attraction of predators as well as woodborers (Miller et al. 2015, 2017) and bark and ambrosia beetles (Miller and Sweeney 2022) show the likelihood of numerous players occurring at the same time on the same hosts. Studying the chemical ecology of the interactions among all these species may provide some insights into critical ecological associations and roles.

In southeastern United States, *T. virescens* is an important predator of bark beetles that infest pine trees (Schoeller and Allison 2013). Solomon (1995) reports *T. virescens* feeding on *Xylotrechus nauticus* (Mannerheim) and *Neoclytus acuminatus* (F.) (Coleoptera: Cerambycidae). As reported by Miller et al. (2015), traps baited with 3-hydroxyhexan-2-one were attractive to *T. virescens* with ethanol enhancing the attraction (Figs. 1A, 2A–B, 3A–B, 4A–B). We found no effects of *syn*-2,3-hexanediol or 3-hydroxyoctan-2-one on responses of *T. virescens*. The response profile of *T. virescens* mirrors that of five common species of longhorn beetles in Georgia: *Anelaphus pumilus* (Newman), *Euderces pini* (Olivier), *Knulliana cincta* (Drury), *Neoclytus mucronatus* (F.) and *Neoclytus scutellaris* (Olivier) (Coleoptera: Cerambycidae) (Miller et al. 2015, 2017).

Larvae of Cleridae, e.g., *Thanasimus formicarius* L., have been reported to feed on cerambycid larvae (Kemner 1913, Gauss 1954). Solomon (1995) mentions a *Chariessa* sp. (Cleridae) as a predator of adult *N. acuminatus* in the United States. In western United States, *Chariessa elegans* Horn (Coleoptera: Cleridae) preys on *Neoclytus conjunctus* (LeConte) (Coleoptera: Cerambycidae) (Furniss and Carolin 1980). *Chariessa pilosa* is common through most of Canada and the United States, and generally associated with hardwood trees (Opitz 2017). Similarly, *N. acuminatus* is associated with numerous species of hardwood trees (Lingafelter 2007). In long-term study of bark and ambrosia beetles, Williams and Ginzel (2020) noted significant numbers of *N. acuminatus* and *C. pilosa*, along with numerous other species, in plantations of eastern black walnut *Juglans nigra* L. in Indiana.

As in Miller et al. (2015, 2022), traps baited with *syn*-2,3-hexanediol were attractive to *C. pilosa* (Figs. 1B, 2C, 3C–D, 4C). The response profile of *C. pilosa* mirrors that of *Anelaphus villosus*, *N. acuminatus*, *Neoclytus jouteli,* and *Megacyllene caryae* (Miller et al. 2015, 2017). Similar to *A. villosus* (Miller et al. 2017) and *N. acuminatus* (Hanks et al. 2012, Wong et al. 2012), attraction of *C. pilosa* to *syn*-2,3-hexanediol was interrupted by the addition of 3,2-hydroxyketones (Figs. 2C, 3C) (Miller et al. 2022).

Assassin bugs such as *Apiomerus* spp. are typically generalist predators and ambush prey on or around flowers. In addition

to bees and flies, acceptable prey of *A. crassipes* include beetle species in several Coleoptera families including Cantharidae, Cerambycidae, Chrysomelidae, Coccinellidae, Curculionidae, Elateridae, and Lampyridae (Swadener and Yonke 1973). In the field, Blatchley (1926) reported *Gaurotes cyanipennis* (Say) (Coleoptera: Cerambycidae) as a prey of *A. crassipes*. As many cerambycids exhibit mimicry of bee and wasp body color patterns, it is not surprising that assassin bugs would prey on them. Moreover, *A. crassipes* were more abundant in traps (baited with the cerambycid pheromones) in the forest canopy than in the understory, consistent with preference for flowering trees (Miller et al. 2020). As in Miller et al. (2015, 2022), *A. crassipes* is broadly attracted to racemic 3-hydroxyhexan-2-one and racemic 3-hydroxyoctan-2-one (Figs. 1C, 2D, 3E–F) with some enhancement by the addition of *syn*-2,3-hexanediols in one study (Fig. 4D). The response profile allows *A. crassipes* to respond to any of the numerous species of cerambycids using hydroxyketones as attractants or pheromones in Georgia (Miller et al. 2015, 2017, 2022).

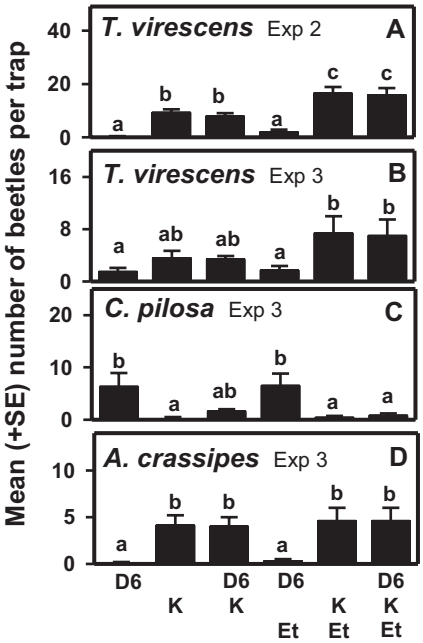

Fig. 2. Effects of *syn*-2,3-hexanediol lure (**D6**), 3-hydroxyhexan-2-one + 3-hydroxyoctan-2-one lures (**K**), and ethanol lures (**Et**) on trap catches of *Temnoscheila virescens* in Experiments 2 (**A**) and 3 (**B**), *Chariessa pilosa* in Experiment 3 (**C**), and *Apiomerus crassipes* in Experiment 3 (**D**). For each species, means followed by the same letter are not significantly different at $P \leq 0.05$ (Holm-Sidak multiple-comparison test).

The role of hexanediols and hydroxyketones as kairomones is the simplest explanation for the attraction of predators to woodboring species with predators eavesdropping on the pheromone channels of woodborers (Imrei et al. 2022). Responding broadly to these compounds allows predators to collocate with numerous species of prey. This may be true for parasitoid species as well. In Illinois, Johnson et al. (2021) found that the parasitoid *Wroughtonia ligator* (Say) (Hymenoptera: Braconidae) was attracted to traps baited with *syn*-2,3-hexanediol, the pheromone for its cerambycid host *N. acuminatus*. However, it is possible that these compounds may also be used as pheromones by these same species. Very little work has been done to identify pheromones for predator and parasitoid species that attack cerambycids (El-Sayed 2021).

Eavesdropping on pheromone channels of cerambycids may also be true for other woodboring species associated with cerambycids such as ambrosia and bark beetles (Curculionidae) and powderpost beetles (Bostrichidae). Both groups typically invade the sapwood of dead or dying trees (USDA 1985). Previously, we reported that catches of five species of bark and ambrosia beetles were enhanced by the addition of 3-hydroxyhexan-2-one and/or 3-hydroxyoctan-2-one in these same studies (Miller and Sweeney 2022).

As in Miller et al. (2015, 2022), we found that *X. basilaris* was strongly attracted to traps baited with *syn*-2,3-hexanediols and weakly attracted to traps baited with the hydroxyketone blend (Fig. 3G–H). Catches in traps baited with the 4-component blend were only reduced by the elimination of *syn*-2,3-hexanediols (Fig. 4E–F). In Miller et al. (2015), *X. basilaris* was attracted to 3-hydroxyhexan-2-one but not 3-hydroxyoctan-2-one. The broad attraction of *X. basilaris* to *syn*-2,3-hexanediols and 3-hydroxyhexan-2-one, emitted by males of several longhorn beetle species in the subfamily Cerambycinae that attack recently dead trees (Hanks and Millar 2016) should increase its chances of finding suitable hosts. Haack (2020) reared specimens of *X. basilaris* as well as four species of cerambycids from branches of shagbark hickory, including *N. acuminatus* which uses *syn*-2,3-hexanediols as its sex/aggregation pheromone (Lacey et al. 2004).

In summary, we found three species of generalist predators of bark and woodboring beetles responding to the same lures that

Table 5. ANOVA Table for effects of *syn*-2,3-hexanediol treatment (**D6**), 3,2-hydroxyketone treatment (**K**), and the interaction between the two treatments (**D6 × K**) for beetle species (Coleoptera) affected by lure treatments in Experiments 4–5

		D6		K		D6 × K	
Species	Exp	$F_{1,27}$	*P*	$F_{1,27}$	*P*	$F_{1,27}$	*P*
Coleoptera: Bostrichidae							
Xylobiops basilaris	4	280.2	<0.001	10.05	0.004	20.56	<0.001
	5	65.58	<0.001	1.562	0.222	9.160	0.005
Coleoptera: Cleridae							
Chariessa pilosa	4	42.77	<0.001	1.802	0.191	8.257	0.008
	5	8.765	0.006	0.009	0.925	11.31	0.002
Coleoptera: Trogossitidae							
Temnoscheila virescens	4	0.155	0.697	60.09	<0.001	3.384	0.077
	5	0.143	0.708	41.32	<0.001	0.375	0.546
Hemiptera: Reduviidae							
Apiomerus crassipes	4	0.009	0.925	718.0	<0.001	0.059	0.810
	5	0.007	0.933	12.73	0.001	0.007	0.933

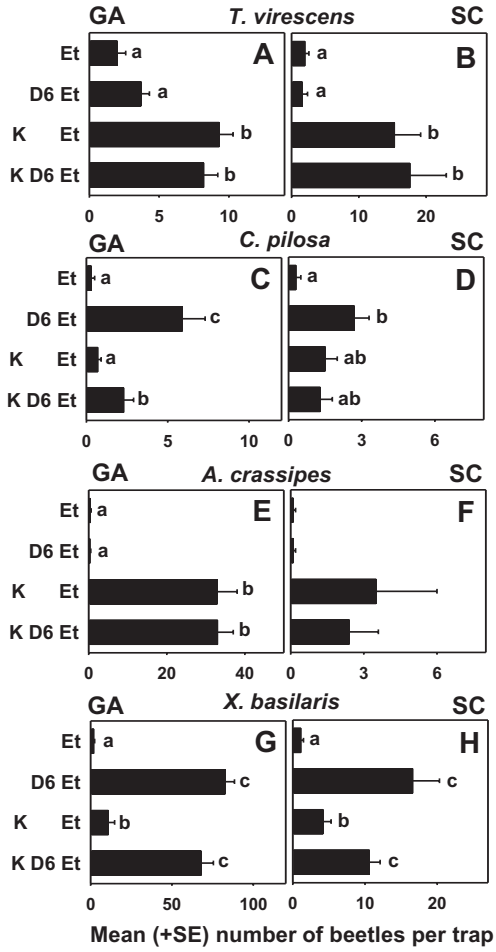

Fig. 3. Effects of *syn*-2,3-hexanediol lure (**D6**), 3-hydroxyhexan-2-one lure + 3-hydroxyoctan-2-one lure (**K**) on catches of *Temnoscheila virescens* (**A–B**), *Chariessa pilosa* (**C–D**), *Apiomerus crassipes* (**E–F**), and *Xylobiops basilaris* (**G–H**) in traps baited with ethanol (**Et**) in Georgia (**GA**) and South Carolina (**SC**) (Experiments 4–5). For each species, means followed by the same letter are not significantly different at $P \leq 0.05$ (Holm-Sidak multiple-comparison test).

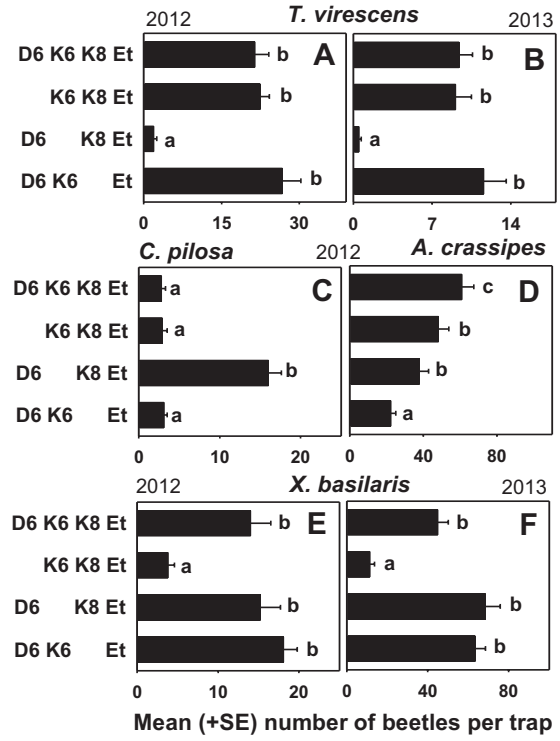

Fig. 4. Effects of eliminating *syn*-2,3-hexanediol (**D6**), 3-hydroxyhexan-2-one (**K6**), and 3-hydroxyoctan-2-one (**K8**) from traps baited with ethanol (**Et**) + D6 + K6 + K8 on catches of *Temnoscheila virescens* (**A–B**), *Chariessa pilosa* (**C**), *Apiomerus crassipes* (**D**), and *Xylobiops basilaris* (**E–F**) in Georgia in 2012 and 2013 (Experiments 6–7). For each species, means followed by the same letter are not significantly different at $P \leq 0.05$ (Holm-Sidak multiple-comparison test).

attract several species of cerambycids, likely placing them all at the same place at the same time. It is possible that adult predators simply prey on adult cerambycids as well as on adult beetles of other species that might be wandering on flowers, branches, and tree trunks. If so, how often do such encounters occur and does it justify the strong behavioral responses of these three predator species? Additionally, it is

Table 6. Mean (±SE) number per trap, and ***F*** and ***P*** values (ANOVA) for beetle species (Coleoptera) not affected by lure treatments in Experiments 1–7

Family, Species	Exp	df	Mean ± SE	$F_{3,27}$	*P*
Buprestidae					
Acmaeodera tubulus	4	3, 27	3.7 ± 0.5	1.297	0.296
Chalcophora virginiensis	4	3, 27	2.9 ± 0.3	0.724	0.547
Elateridae					
Alaus myops	1	7, 49	0.5 ± 0.1	0.718	0.657
Passandridae					
Catogenus rufus	1	7, 49	0.5 ± 0.1	0.611	0.744
	3	5, 35	1.3 ± 0.2	0.511	0.766
	6	3, 24	2.1 ± 0.3	2.705	0.068
	7	3, 27	1.3 ± 0.2	1.375	0.271
Trogossitidae					
Corticotomus depressus	3	5, 35	1.8 ± 0.2	0.817	0.546
Tenebroides spp	1	7, 49	1.7 ± 0.2	1.664	0.140
	2	5, 35	4.4 ± 0.4	1.574	0.193
	3	5, 35	4.6 ± 0.4	2.315	0.064
	4	3, 37	2.9 ± 0.3	0.821	0.494
	6	3, 24	9.5 ± 0.6	0.515	0.676
	7	3, 27	2.5 ± 0.3	0.268	0.848

possible that larval predators prey on larval cerambycids. However, is the timing of responses by adults sufficient to allow for larval prey to be available in sufficient numbers for larval predators, such as with various species of bark beetles that colonize hosts in mass numbers? Might females lay multiple eggs on the same host over time? Is it possible that females of other cerambycid species also lay eggs on the same host?

As generalist predators, larval predators may also feed on non-cerambycid species in their larval stages. The bostrichid *X. basilaris* is attracted to *syn*-2,3-hexanediol (Figs. 3G–H, 4E–F; Miller et al. 2015) whereas the bark beetle *Hypothenemus rotundicollis* (Eichhoff) (Coleoptera: Curculionidae) is attracted to 3-hydroxyoctan-2-one (Miller and Sweeney 2022, Miller et al. 2022). Ambrosia beetles are broadly attracted to ethanol (Miller and Rabaglia 2009); ethanol also enhances attraction of some cerambycids (Miller et al. 2017). Attraction of some ambrosia beetles is enhanced by the presence of hydroxyketones (Miller and Sweeney 2022, Miller et al. 2022).

And finally, if *T. virescens*, *C. pilosa*, and *A. crassipes* are generalist predators then why the difference in specificity among the three species? Is interspecific competition a factor between predator species? And lastly, there is always the possibility that these compounds are used as pheromones by these predators. Sex pheromones have not been identified for species in any of these predator families but that may be due to lack of research on the chemical ecology of predators rather than lack of pheromone use by those species. Considerable research effort will be required to answer these questions. Our results help to identify three species of predators that could be the foci for such studies.

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