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# Sulcatol: Enantiospecific Attractant for *Monarthrum mali* (Coleoptera: Curculionidae: Scolytinae), *Leptostylus asperatus* (Coleoptera: Cerambycidae) and Associated Predators

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## Abstract

In 2014–2019, we conducted six experiments in north-central Georgia in an attempt to verify the aggregation pheromone response of the ambrosia beetle *Gnathotrichus materiarius* (Fitch) (Coleoptera: Curculionidae: Scolytinae: Scolytini: Corthylina) to sulcatol known to be produced by male *G. materiarius*; we failed to catch any *G. materiarius*. However, we did find that another corthyline ambrosia beetle species *Monarthrum mali* (Fitch) was attracted to (*R*)-(–)-sulcatol, whereas the longhorn beetle *Leptostylus asperatus* (Haldeman) (Coleoptera: Cerambycidae: Lamiinae) was attracted to (*S*)-(+)-sulcatol. Attraction of both species was unaffected by the respective antipodes. Ethanol enhanced attraction of both species to traps baited with sulcatol. In at least one experiment, attraction to ethanol-baited traps was enhanced by sulcatol for *Xylosandrus crassiusculus* (Motschulsky), *Xyleborus* spp., and *Hypothenemus* spp. but reduced for *Cnestus mutilatus* (Blandford) (Coleoptera: Curculionidae: Scolytinae). Additionally, traps baited with ethanol and racemic sulcatol [50% (*S*)-(+): 50% (*R*)-(-)] caught the greatest numbers of four species of beetle predators: *Coptodera aerata* Dejean (Coleoptera: Carabidae), *Colydium lineola* Say (Coleoptera: Zopheridae), *Madoniella dislocata* (Say), and *Pyticeroides laticornis* (Say) (Coleoptera: Cleridae). Ethanol but not sulcatol attracted *Temnoscheila virescens* (F.) (Coleoptera: Trogossitidae). Information on interspecific relationships within forested communities may help us to better determine the roles of these species in maintaining stable and resilient forested ecosystems.

**Key words:** sulcatol, enantiomeric composition, ambrosia beetles, woodborers

From the perspective of chemical ecology, ambrosia beetles can be divided broadly into two groups based on their mating systems. The first group include the Xyleborina (Curculionidae: Scolytinae: Scolytini) which are typically haplodiploid (Kirkendall 1983, Jordal et al. 2000). Males are uncommon, diminutive, and flightless. Dispersal and host colonization is done by females, largely attracted to kairomones such as ethanol and α-pinene to locate hosts (Miller and Rabaglia 2009, Ranger et al. 2016). The use of sex or aggregation pheromones has not been documented within this group, likely due to the fact that females are able to colonize new hosts without the need of a mate from outside their source breeding sites (Jordal et al. 2000).

In contrast, aggregation pheromones are common among the second group of ambrosia beetles consisting of diploid species such as the Corthylina (Curculionidae: Scolytinae: Scolytini) (Kirkendall 1983). In western North America, two corthyline species *Gnathotrichus sulcatus* (LeConte) and *Gnathotrichus retusus* (LeConte) attack and breed in dead, dying or downed woody material, including lumber in wood-processing areas (Shore 1992, Daterman and Overhulser 2002). Males of both species locate susceptible hosts, initiate galleries in the wood, and produce the aggregation pheromone sulcatol (6-methyl-5-hepten-2-ol) that attracts conspecific females and males (Byrne et al. 1974, Borden and McLean 1979). The enantiomeric composition of sulcatol used by *G. sulcatus* is 65% (*S*)-(+): 35% (*R*)-(–), whereas *G. retusus* uses (*S*)-(+)-sulcatol (= retusol) alone (Byrne et al. 1974; Plummer et al. 1976; Borden et al. 1976, 1980a, 1981).

Males of the eastern North American species *Gnathotrichus materiarius* (Fitch) also produce sulcatol but with an enantiomeric composition of 31% (*S*)-(+): 69% (*R*)-(–) (Fletchmann and Berisford 2003). Behavioral attraction of *G. materiarius* to sulcatol has not been demonstrated to date. Therefore, the objective of this study was

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to determine the flight responses of *G. materiarius* to traps baited with sulcatol in the southeastern United States. We also documented the responses of other species of bark and woodboring beetles (and their predators) to sulcatol. In North America, a few pheromones such as 2,3-hexanediol and 3-hydroxyhexane-2-one produced by some longhorn beetles (Cerambycidae), and ipsdienol and ipsenol produced by some bark beetles (Curculionidae: Scolytinae), are known to be broadly attractive to numerous species of bark and woodboring beetles (and associated predators), acting either as pheromones or kairomones (Allison et al. 2013; Hanks and Millar 2013, 2016; Hanks et al. 2014, 2018; Millar et al. 2018; Miller et al. 2013a, 2015a, b; Ray et al. 2015). The same may be true for sulcatol as well. Information on interspecific relationships within forested communities may help us to better determine the roles of these species in maintaining stable and resilient forested ecosystems.

## Materials and Methods

Six randomized-block trapping experiments were conducted in north-central Georgia during the period of 2013–2019 with various sulcatol and ethanol lure treatments (Table 1). The objective of experiments 1, 2, 4, and 5 was to identify species with responses to racemic [50% (+): 50% (–)] and (+)-sulcatol comparable to the western species of *Gnathotrichus*, whereas experiment 3 tested both enantiomers of sulcatol as well as racemic sulcatol. Ethanol is a general attractant for ambrosia beetles in southeastern United States (Miller and Rabaglia 2009), and enhances attraction of *G. retusus* and *G. sulcatus* to traps baited with sulcatol in British Columbia (Borden et al. 1980b). The objective of experiment 6 was to identify the role of ethanol for beetles that were attracted to the combination of ethanol and sulcatol in experiments 1–5.

The experiments were set in mixed stands of mature *Pinus taeda* L., *Pinus echinata* Miller, *Quercus alba* L, *Quercus falcata* Michaux, *Liquidambar styraciflua* L., and *Carya tomentosa* Sargent at the Scull Shoals Experiment Forest (33.7361°N, 83.2736°W) near Maxeys, GA (experiments 1, 3, 5, and 6), the Oconee National Forest (33.2333°N, 83.5204°W) near Eatonton, GA (experiment 2), and the Charlie Elliott Wildlife Center (33.4623°N, 83.7333°W) near Mansfield, GA (experiment 4). Ethanol UHR pouch lures and sulcatol bubblecap lures [(+), (–) and racemic] were obtained from Contech Enterprises (Delta, BC). Chemical purities were >95% for ethanol lures and >99% for sulcatol lures. Enantiopurities of (+)- and (–)-sulcatol lures were >99%. Release rates for ethanol and sulcatol lures were 0.5 g/d and 5 mg/d at 24°C, respectively (determined by manufacturer). Black multiple-funnel traps (Synergy Semiochemicals Inc., Burnaby, BC) were hung on twine strung between trees at a spacing of 10–15 m between traps (within and between blocks) and a buffer distance of ≥2m to any tree. Two funnels were removed from each 12-unit multiple-funnel trap to make it easier to hang the traps while ensuring that collection cups were kept 0.5–1.0 m above ground level. Each trap was modified by expanding the bottom of each funnel from 5 to 12 cm as in Miller et al. (2013b), producing 10-unit traps that allow lures to be hung within the funnels. Hanging lures within the funnels of a multiple-funnel trap can increase catches of beetles by 50–400% (Miller et al. 2013b). Collection cups contained RV & Marine Antifreeze (SPLASH Products Inc., St. Paul, MN in 2013–2016, and Winter-Eez, Southwind Ltd, Greensboro, NC in 2019) to preserve insects until collection (Miller and Duerr 2008). Trap catches were collected every 2 wk with fresh antifreeze added to each cup on each occasion. Voucher specimens were deposited in the UGA Collection of Arthropods (University of Georgia, Athens, GA) and retained at USDA Forest Service (Southern Research Station, Athens, GA).

Analyses on total trap catches for each species per experiment were conducted with the SYSTAT (ver. 13) and the SigmaStat (ver. 3.01) statistical packages (SYSTAT Software Inc., Point Richmond, CA) for each species caught in total numbers ($N$) ≥ 25 within an experiment. Data in experiments 1, 2, 4, and 5 were analyzed by two-tailed paired $t$ test. Normality was verified by the Shapiro–Wilk test. Data in experiments 3 and 6 were analyzed by mixed-model ANOVA using block as a random factor and treatment as a fixed factor, followed by the Holm–Sidak multiple-comparison test ($\alpha \leq 0.05$) which controls the experiment-wise error rate at 0.05 (Glantz 2005). Data for species with a significant treatment effect in experiment 6 were also analyzed by mixed-model ANOVA using block as a random factor, and ethanol treatment (Et), sulcatol treatment (S), and the interaction between Et and S as fixed factors. Trap catch data for experiments 3 and 6 were transformed as needed by $\ln(Y + 1)$ to ensure normality and homoscedasticity (Pepper et al. 1997), verified by the Shapiro–Wilk and Levene's tests, respectively.

## Results

### Ambrosia Beetles (Curculionidae)

We did not capture any *G. materiarius* in our experiments. However, sulcatol did have an effect on several other species of ambrosia beetles. In experiments 2 and 4, catches of *Monarthrum mali* (Fitch) in traps baited with ethanol + racemic sulcatol were greater than those in traps baited solely with ethanol (Fig. 1A and B). In experiment 3, catches of *M. mali* in ethanol-baited traps increased with the addition of racemic sulcatol or (–)-sulcatol but not (+)-sulcatol (Fig. 2A). In experiment 6, both ethanol and sulcatol increased catches of *M. mali* with a synergistic interaction between the two treatments (Table 2). Catches of *M. mali* were highest in traps baited with both ethanol and sulcatol (Fig. 3A).

Catches of *Cnestus mutilatus* (Blandford) in experiment 6 were affected by ethanol and racemic sulcatol (Table 2) with catches greater in traps baited with ethanol than those without ethanol

**Table 1.** Treatments, number of blocks ($n$), and trapping periods for six randomized-block experiments conducted with sulcatol and ethanol in northcentral Georgia

| Exp | $n$ | Trapping Period | Treatments |
|---|---|---|---|
| 1 | 4 | 20 April–12 June 2013 | 1. Ethanol UHR lure [Et] 2. (+)-Sulcatol lure [(+) S] + Et lure |
| 2 | 6 | 20 May–2 July 2013 | 1. Et lure 2. Racemic sulcatol lure [S] + Et lure |
| 3 | 10 | 27 June–9 Sept. 2014 | 1. Et lure 2. (+) S lure + Et lure<br>3. S lure + Et lure 4. (-)-Sulcatol lure [(-) S] + Et lure |
| 4 | 10 | 8 July–11 Sept. 2014 | 1. Et lure 2. Racemic sulcatol lure [S] + Et lure |
| 5 | 8 | 26 Sept.–5 Nov. 2016 | 1. Ethanol UHR lure [Et] 2. (+)-Sulcatol lure [(+) S] + Et lure |
| 6 | 9 | 26 April–30 July 2019 | 1. Blank control [Blank] 2. Et lure 3. S lure 4. S lure + Et lure |

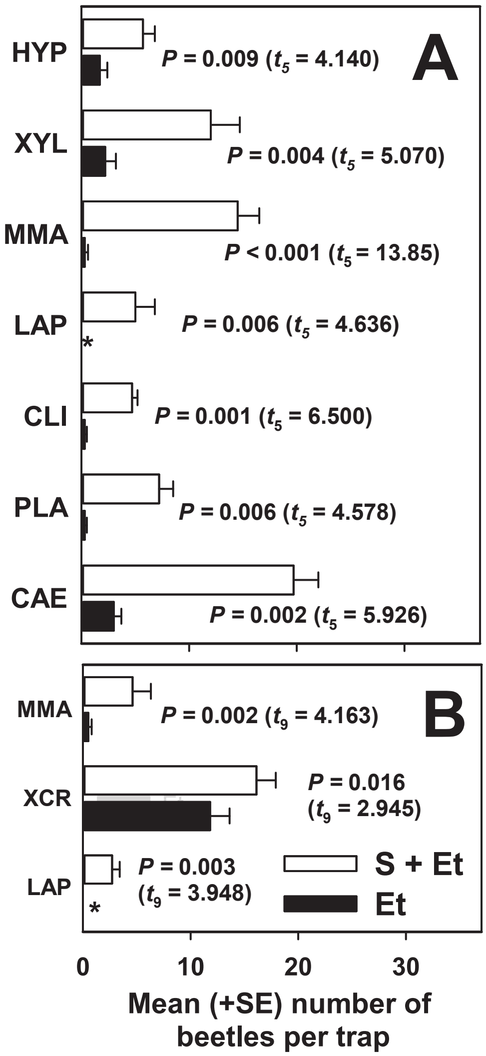

**Fig. 1.** Effects of racemic sulcatol (S) on catches of *Hypothenemus* spp. (HYP; $n$ = 44), *Xyleborus* spp. (XYL; $n$ = 85), *Monarthrum mali* (MMA; $n$ = 89), *Leptostylus asperatus* (LAP; $n$ = 30), *Colydium lineola* (CLI; $n$ = 30), *Pyticeroides laticornis* (PLA; $n$ = 45), and *Coptodera aerata* (CAE; $n$ = 136) in experiment 2 (A), and *M. mali* ($n$ = 51), *L. asperatus* ($n$ = 27) and *Xylosandrus crassiusculus* (XCR; $n$ = 279) in experiment 4 (B) in traps baited with ethanol (Et). Treatment with an asterisk had zero catches. $P$ = significance level (paired $t$ test). $N$ = total number caught.

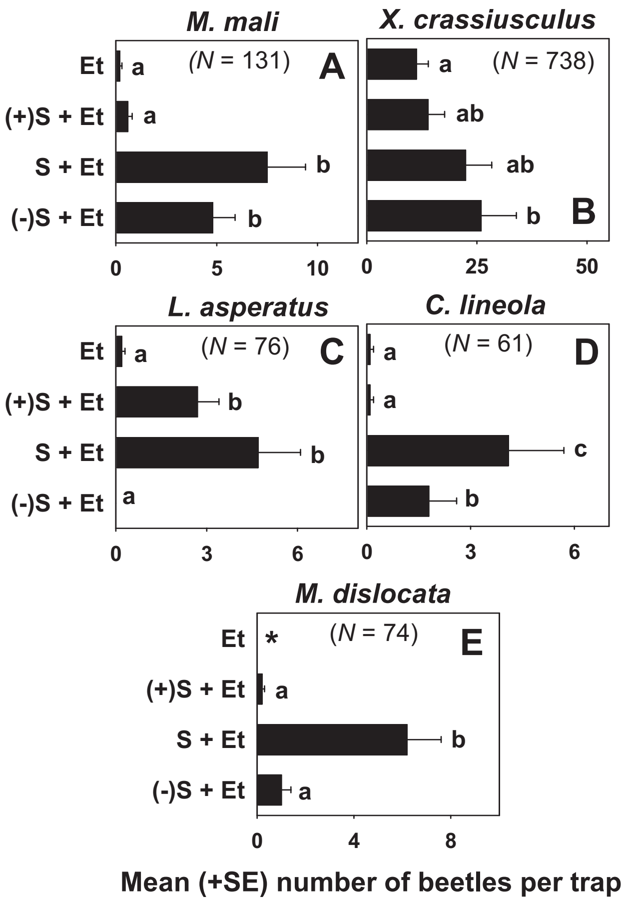

**Fig. 2.** Effects of (+)-sulcatol [(+)S], racemic sulcatol [S], and (–)-sulcatol [(-)S] on catches of (A) *Monarthrum mali* ($F_{3,27}$ = 26.29; $P < 0.001$), (B) *Xylosandrus crassiusculus* ($F_{3,27}$ = 4.247; $P < 0.014$), (C) *Leptostylus asperatus* ($F_{3,27}$ = 26.03; $P < 0.001$), (D) *Colydium lineola* ($F_{3,27}$ = 13.28; $P < 0.001$), and (E) *Madoniella dislocata* ($F_{3,27}$ = 28.33; $P < 0.001$) in traps baited with ethanol (Et) in experiment 3. Means followed by the same letter are not significantly different at $P$ = 0.05 (Holm–Sidak test). $N$ = total number caught.

(Fig. 3B). The addition of sulcatol reduced catches of *C. mutilatus* in ethanol-baited traps (Fig. 3B). Sulcatol had no effect on catches of *C. mutilatus* in experiments 1–3 (Tables 3 and 4). Racemic sulcatol increased catches of *Xylosandrus crassiusculus* (Motschulsky) in experiment 4 (Fig. 1B) but not in experiment 2 (Fig. 1A). Catches of *Xyleborus* spp. in ethanol-baited traps were increased with the addition of racemic sulcatol in experiment 2 (Fig. 1A) but unaffected by sulcatol (regardless of enantiomeric composition) in experiment 3 (Table 4).

Racemic sulcatol had no effect on catches of *Dryoxylon onoharaense* (Murayama) and *Xyleborinus saxesenii* (Ratzeburg) in experiment 2 nor on *D. onoharaense* in experiment 4 (Table 3). Similarly, (+)-sulcatol had no effect on catches of *Cyclorhipidion bodoanum* (Reitter), *C. mutilatus*, *D. onoharaense*, *X. crassiusculus*, and *X. saxesenii* in experiment 1 (Table 3). In experiment 3, sulcatol (regardless of enantiomeric composition) had no effect on catches of *Ambrosiodmus* spp., *C. bodoanum*, *C. mutilatus*, *D. onoharaense*, and *X. saxesenii* (Table 4). Catches of *Ambrosiophilus atratus* (F.), *Euwallacea interjectus* (Blandford) and *Xylosandrus germanus* (Blandford) were unaffected by ethanol and sulcatol treatments in experiment 6 (Table 4).

Ethanol affected catches of *D. onoharaense*, *X. crassiusculus*, *X. saxesenii*, and *Xyleborus* spp. in experiment 6 (Table 2). Catches of these species were greatest in traps baited with ethanol, regardless of the addition of sulcatol (Fig. 3C–F). Ethanol (but not sulcatol) had a negative effect on catches of *Ambrosiodmus* spp. (Table 2) with catches lower in traps baited with ethanol + sulcatol than in those baited with sulcatol alone (Fig. 3G).

## Bark and Snout Beetles (Curculionidae)

The abundance and diversity of bark and snout beetles was low in our study with no significant catches of *Dendroctonus*, *Hylastes*, *Hylobius*, *Ips*, or *Orthotomicus* spp. Catches of the twig beetles *Hypothenemus* spp. in experiment 2 were greater in traps baited with ethanol + racemic sulcatol than in traps baited solely with ethanol (Fig. 1A); treatments had no effect on *Hypothenemus* spp. in experiment 3 (Table 4). Ethanol but not sulcatol affected trap catches of *Hypothenemus* spp. in experiment 6 (Table 2). Beetle catches in traps baited with ethanol alone or ethanol + sulcatol were greater than those in blank control traps (Fig. 3I). There was no treatment effect

**Table 2.** ANOVA results for effects of ethanol (Et), racemic sulcatol (S), and the interaction between the two treatments (Et × S) on trap catches of beetle species affected by treatments in experiment 6

| Family Species | Et | | S | | Et × S | |
|---|---|---|---|---|---|---|
| | $F_{1,24}$ | $P$ | $F_{1,24}$ | $P$ | $F_{1,24}$ | $P$ |
| Carabidae *C. aerata* | 31.26 | <0.001 | 44.25 | <0.001 | 3.772 | 0.064 |
| Cerambycidae *L. asperatus* | 12.27 | 0.002 | 167.3 | <0.001 | 2.300 | 0.142 |
| Cleridae *M. dislocata* | 29.66 | <0.001 | 123.4 | <0.001 | 2.818 | 0.106 |
| *P. laticornis* | 34.10 | <0.001 | 35.61 | <0.001 | 2.739 | 0.111 |
| Curculionidae *Ambrosiodmus* spp | 15.34 | <0.001 | 0.102 | 0.752 | 2.335 | 0.140 |
| *C. mutilatus* | 737.9 | <0.001 | 7.598 | 0.011 | 4.149 | 0.053 |
| *D. onoharaense* | 160.1 | <0.001 | 0.014 | 0.907 | 0.187 | 0.669 |
| *Hypothenemus* spp | 18.32 | <0.001 | 1.193 | 0.286 | 3.636 | 0.069 |
| *M. mali* | 77.09 | <0.001 | 64.61 | <0.001 | 20.66 | <0.001 |
| *X. crassiusculus* | 287.1 | <0.001 | 0.286 | 0.598 | 1.974 | 0.173 |
| *X. saxesenii* | 118.7 | <0.001 | 3.963 | 0.058 | 0.409 | 0.528 |
| *Xyleborus* spp | 12.83 | 0.002 | 2.039 | 0.166 | 0.685 | 0.416 |
| Trogossitidae *T. virescens* | 35.39 | <0.001 | 0.437 | 0.515 | 1.374 | 0.253 |
| Zopheridae *C. lineola* | 5.650 | 0.026 | 21.42 | <0.001 | 1.648 | 0.212 |

on catches of *Cossonus* spp., *Dryophthorus americanus* Bedel, and *Stenoscelis brevis* (Boheman) in experiment 6 (Table 4).

### Longhorn Beetles (Cerambycidae)

The longhorn beetle *Leptostylus asperatus* (Haldeman) was clearly affected by sulcatol in all six experiments. In experiments 1, 2, 4, and 5, catches of *L. asperatus* were greater in traps baited with ethanol + racemic sulcatol (Fig. 1A and B) or ethanol + (+)-sulcatol (Fig. 4) than in traps baited solely with ethanol. In experiment 3, catches in traps baited with ethanol + (+)-sulcatol or ethanol + racemic sulcatol were greater than those in traps baited with ethanol alone or ethanol + (−)-sulcatol (Fig. 2C). In experiment 6, catches of *L. asperatus* were affected by both ethanol and sulcatol with no significant interaction between the two treatments (Table 2). Traps baited with sulcatol caught more beetles than those not baited with sulcatol; catches of *L. asperatus* were greatest in those traps baited with both ethanol and sulcatol (Fig. 3H). *Xylotrechus colonus* (F.) in experiment 6 was unaffected by trap treatments (Table 4). None of 38 other species of Cerambycidae detected in our study was caught in sufficient numbers for analyses. However, results in experiment 6 suggest a possible effect of sulcatol on catches of *Aegomorphus modestus* (Gyllenhal); 16 of 18 beetles were captured in traps baited with sulcatol alone (7) or ethanol + sulcatol (9).

### Beetle Predators

Beetle species from five families of beetle predators were detected in sufficient numbers for analyses in our study. In experiment 2, trap catches of *Coptodera aerata* Dejean (Carabidae), *Colydium lineola* Say (Zopheridae), and *Pyticeroides laticornis* (Say) (Cleridae) were greater in traps baited with ethanol + racemic sulcatol than in traps baited solely with ethanol (Fig. 1A). In experiment 3, catches of *C. lineola* were greatest in traps baited with ethanol + racemic sulcatol (Fig. 2D); traps baited with ethanol and (−)-sulcatol caught more beetles than those baited with ethanol alone or ethanol + (+)-sulcatol. Traps baited with ethanol + racemic sulcatol caught more *Madoniella dislocata* (Say) (Cleridae) than traps with all other treatments in experiment 3 (Fig. 2E).

In experiment 6, catches of *C. aerata*, *C. lineola*, *M. dislocata*, and *P. laticornis* were affected by both ethanol and sulcatol treatments with no interaction between treatments (Table 2). For all four species, traps baited with ethanol + racemic sulcatol caught the most beetles (Fig. 5A–D). There was no difference in catches of *C. lineola* among the remaining three treatments (Fig. 5B). Catches of *M. dislocata* in traps baited with racemic sulcatol alone were greater than those in traps baited with ethanol alone; catches for both treatments were greater than those in blank control traps (Fig. 5A). Catches of *P. laticornis* and *C. aerata* in traps baited with ethanol alone were no different from those in traps baited with racemic sulcatol alone; both were greater than catches in blank control traps (Fig. 5C and D).

Ethanol but not racemic sulcatol affected trap catches of *Temnoscheila virescens* (F.) (Trogossitidae) in experiment 6 (Table 2). Catches were greatest in traps baited with ethanol, regardless of the addition of sulcatol (Fig. 5E). Treatments had no effect on catches of *Tenebroides* spp. (Trogossitidae) and *Namunaria guttulata* (LeConte) (Zopheridae) in experiment 2 (Table 3), *T. virescens* and *Tenebroides* spp. in experiment 3 (Table 4), and *Catogenus rufus* (F.) (Passandridae) and *Tenebroides* spp. in experiment 6 (Table 4).

## Discussion

The lack of *G. materiarius* in traps baited with sulcatol in our study is disconcerting given the fact that male *G. materiarius* are known to produce sulcatol (Fletchmann and Berisford 2003). Habitat and timing are two factors that may have influenced our lack of success with *G. materiarius* in our trapping studies. We began our studies at different times of the year with the earliest starting in late April. It is possible that we missed the spring flight of *G. materiarius*. Turnbow and Franklin (1980) detected flight activity of *G. materiarius* in northcentral Georgia from February to November with a distinct peak in March. In past studies, we captured *G. materiarius* throughout the summer and fall in northcentral Georgia, although never in large numbers (unpublished data).

Another possibility is that pheromone responses exhibited by *G. materiarius* may require host volatiles such as α-pinene, a compound commonly associated with pine trees (Smith 2000); *G. materiarius* breeds in dead and dying eastern conifers (USDA 1985, Dodds et al. 2017). In one study with ethanol and α-pinene, catches of *G. materiarius* in western North Carolina were weakly affected positively by α-pinene but not ethanol (Miller and Rabaglia 2009). Additionally, *G. materiarius* may be more abundant in pine stands with significant dead, dying, damaged, or downed trees such as those with high populations of *Ips* engraver beetles (USDA 1985). In a

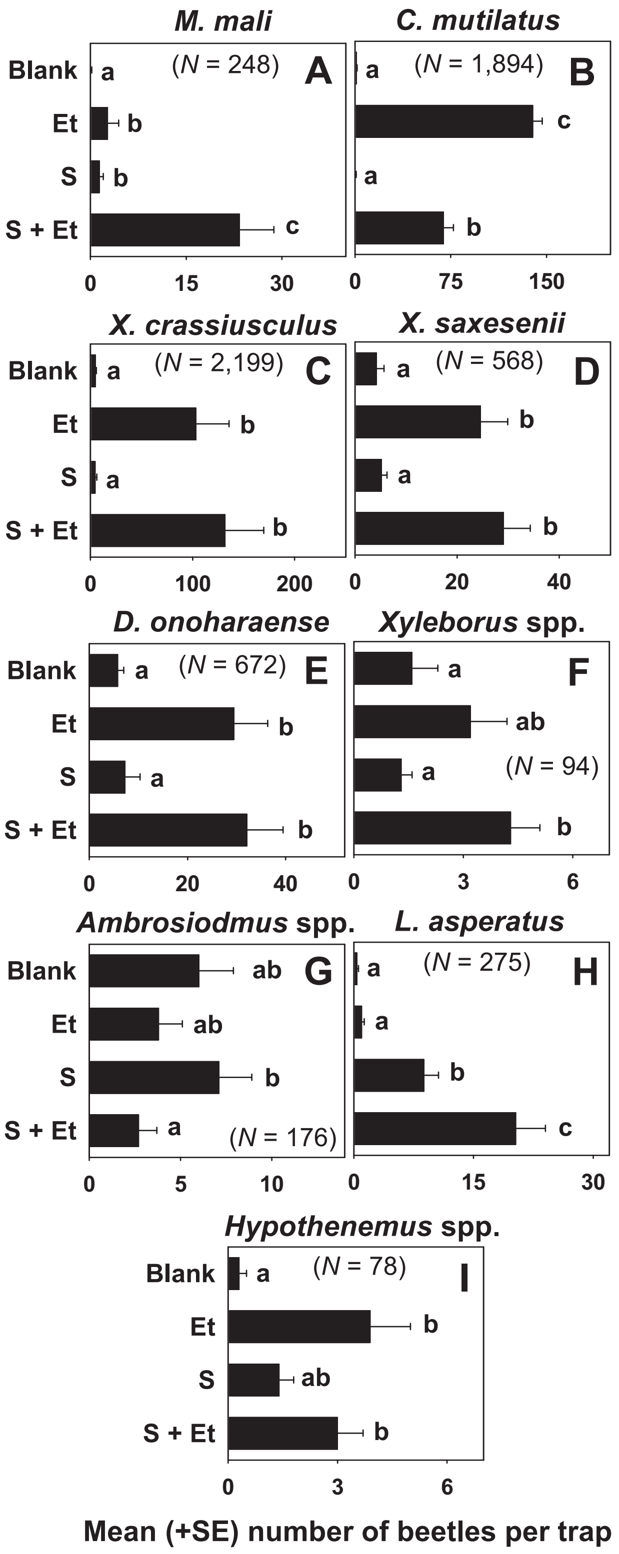

**Fig. 3.** Effects of ethanol (Et) and racemic sulcatol (S) on trap catches of (A) *Monarthrum mali* ($F_{3,24} = 54.12$ $P < 0.001$), (B) *Cnestus mutilatus* ($F_{3,24} = 249.9$; $P < 0.001$), (C) *Xylosandrus crassiusculus* ($F_{3,24} = 11.03$; $P < 0.001$), (D) *Xyleborinus saxesenii* ($F_{3,24} = 41.03$; $P < 0.001$), (E) *Dryoxylon onoharaense* ($F_{3,24} = 53.44$; $P = 0.004$), (F) *Xyleborus* spp. ($F_{3,24} = 5.185$; $P = 0.007$), (G) *Ambrosiodmus* spp. ($F_{3,24} = 5.924$; $P < 0.001$), (H) *Leptostylus asperatus* ($F_{3,24} = 60.62$; $P < 0.001$), and (I) *Hypothenemus* spp. ($F_{3,24} = 7.715$; $P < 0.001$) in experiment 6. Means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test). $N$ = total number caught.

trapping study with *Ips* pheromones (ipsenol, ipsdienol and lanierone) in western North Carolina, ipsdienol resulted in a strong increase in trap catches of *G. materiarius* with a weak effect from ipsenol (Miller et al. 2005). In Virginia, traps baited with the quaternary combination of (ipsenol + ipsdienol) and (ethanol + α-pinene) resulted in greater catches of *G. materiarius* than those baited with either of the two binary blends alone (Miller et al. 2011).

However, traps baited with racemic or (−)-sulcatol were attractive to the ambrosia beetle *M. mali* in Georgia (Table 2; Figs. 1–3). *M. mali* is another corthyline species, one that commonly breeds in various species of eastern hardwoods rather than conifers (USDA 1985, Dodds et al. 2017). Separation by host species would allow the use of sulcatol by both species with little interspecific interaction between these two species. In Ohio, Ranger et al. (2014) noted attraction of the congeneric species *Monarthrum fasciatum* (Say) to traps baited with ethanol and racemic sulcatol but not traps baited with ethanol and (+)-sulcatol; (−)-sulcatol was not tested.

The use of sulcatol as a pheromone is not unique to corthyline species of ambrosia beetles. Males of the South American species *Megaplatypus mutatus* (Chapuis) (Curculionidae: Platypodinae) produce (+)-sulcatol which attracts female *M. mutatus* (Gonzalez-Audino et al. 2005, Gatti et al. 2011). Similarly, a North American platypodine species *Euplatypus flavicornis* F., common in pine stands of the southern United States, uses sulcatol (enantiomeric composition unknown) as a pheromone (Renwick et al. 1977); none were caught in the present study.

The lamiine cerambycid *L. asperatus* was clearly attracted to traps baited with racemic or (+)-sulcatol in our study (Table 2; Figs. 1–4). In eastern North America, Meier et al. (2019) found that males of two lamiine species *Leptostylus transversus* (Gyllenhal) and *Astylopsis macula* (Say) produce (−)-sulcatol as a pheromone; both sexes of each species are attracted to (−)-sulcatol. In addition to sulcatol varying by enantiomeric composition, species separation among lamiine species in North America likely includes other related compounds such as sulcatone, fuscumol, and fuscumol acetate (Meier et al. 2020).

Not surprisingly, we found that several species of predators from three beetle families were attracted to traps baited with sulcatol (Figs. 1, 2, and 5). Beetle predators such as *T. virescens*, *Chariessa pilosa* (Forster) (Coleoptera: Cleridae) and *Apiomerus crassipes* (F.) (Hemiptera: Reduviidae) are known to be attracted to other cerambycid pheromones such as 2,3-hexanediol and 3,2-hydroxyketones (Miller et al. 2015b). However, the association between predators and cerambycids is unclear as several other taxa are also associated with sulcatol as noted earlier. Understanding the competitive interactions between woodborers for use of resources as well as the impacts from predators should help us to better understand the basis for stable and resilient forest ecosystems, particularly with respect to potential impacts from external factors such as climate change, invasive nonnative species, and forest management practices.

Various authors have noted parsimony in the use of pheromones within subfamilies or tribes for Cerambycidae, likely based on evolutionary relationships (Ray et al. 2006, Hanks and Millar 2013, Millar and Hanks 2017). A similar parsimony is found among bark beetles (Curculionidae: Scolytinae) with compounds such as frontalin, brevicomin, ipsenol and ipsdienol acting as common aggregation pheromones (Borden 1982, Byers 2007, El-Sayed 2019). However, it is unclear how the use of sulcatol as a pheromone could have arisen in such disparate taxa as Lamiinae (Cerambycidae), Scolytinae: Corthylina (Curculionidae) and Platypodinae (Curculionidae). Additionally, sulcatol has been found in the hindguts of female *Dendroctonus pseudotsugae* Hopkins (Curculionidae: Scolytinae)

**Table 3.** Statistical results for paired *t* tests, total number caught (*N*), and mean (± SE) number of beetles per trap for species unaffected by the addition of sulcatol to ethanol-baited traps at *P* = 0.05 in experiments 1, 2, and 4

| Exp | Species | *N* | *t* | df | *P* | Mean ± SE |
|---|---|---|---|---|---|---|
| 1 | *C. bodoanum* | 25 | 0.116 | 3 | 0.346 | 3.6 ± 1.1 |
| | *C. mutilatus* | 75 | 2.164 | | 0.119 | 9.4 ± 1.8 |
| | *D. onoharaense* | 51 | 1.890 | | 0.125 | 6.4 ± 1.3 |
| | *X. crassiusculus* | 74 | 0.477 | | 0.666 | 9.3 ± 2.4 |
| | *X. saxesenii* | 82 | 1.414 | | 0.252 | 10.3 ± 2.4 |
| 2 | *C. bodoanum* | 29 | 0.113 | 5 | 0.914 | 2.4 ± 0.6 |
| | *C. mutilatus* | 119 | 0.469 | | 0.659 | 9.9 ± 1.1 |
| | *D. onoharaense* | 142 | 2.390 | | 0.062 | 11.8 ± 1.6 |
| | *X. saxesenii* | 32 | 0.337 | | 0.750 | 2.7 ± 0.6 |
| | *X. crassiusculus* | 247 | 0.536 | | 0.615 | 20.6 ± 5.7 |
| | *Tenebroides* spp. | 36 | 0.466 | | 0.661 | 3.0 ± 0.5 |
| 4 | *D. onoharaense* | 241 | 2.207 | 9 | 0.055 | 12.1 ± 1.0 |
| | *N. guttulata* | 74 | 0.797 | | 0.446 | 3.7 ± 0.8 |
| | *Tenebroides* spp. | 91 | 1.551 | | 0.155 | 4.6 ± 0.6 |

**Table 4.** ANOVA results for treatment effects, total number caught (*N*), and mean (± SE) number of beetles per trap for species unaffected by treatments at *P* = 0.05 in experiments 3 and 6

| Exp | Species | *N* | *F* | df | *P* | Mean ± SE |
|---|---|---|---|---|---|---|
| 3 | *Ambrosiodmus* spp. | 35 | 0.333 | 3, 27 | 0.802 | 0.9 ± 0.2 |
| | *C. bodoanum* | 48 | 0.188 | | 0.904 | 1.2 ± 0.2 |
| | *C. mutilatus* | 140 | 0.742 | | 0.536 | 3.5 ± 0.6 |
| | *D. onoharaense* | 333 | 0.183 | | 0.907 | 8.3 ± 0.8 |
| | *Hypothenemus* spp. | 44 | 1.369 | | 0.273 | 1.1 ± 0.2 |
| | *T. virescens* | 42 | 1.351 | | 0.279 | 1.1 ± 0.2 |
| | *Tenebroides* spp. | 141 | 0.531 | | 0.665 | 3.5 ± 0.3 |
| | *Xyleborus* spp. | 58 | 1.251 | | 0.311 | 1.5 ± 0.2 |
| | *X. saxesenii* | 128 | 0.483 | | 0.697 | 3.2 ± 0.4 |
| 6 | *A. atratus* | 203 | 0.592 | 3, 24 | 0.626 | 0.9 ± 0.2 |
| | *C. rufus* | 36 | 1.007 | | 0.407 | 1.0 ± 0.2 |
| | *Cossonus* spp. | 77 | 1.073 | | 0.379 | 2.1 ± 0.4 |
| | *D. americanus* | 41 | 1.349 | | 0.282 | 1.1 ± 0.2 |
| | *E. interjectus* | 227 | 1.650 | | 0.204 | 6.3 ± 0.8 |
| | *S. brevis* | 977 | 1.070 | | 0.380 | 27.1 ± 3.4 |
| | *Tenebroides* spp. | 156 | 1.591 | | 0.218 | 4.3 ± 0.4 |
| | *X. colonus* | 63 | 2.605 | | 0.075 | 1.8 ± 0.3 |
| | *X. germanus* | 80 | 0.732 | | 0.543 | 2.2 ± 0.3 |

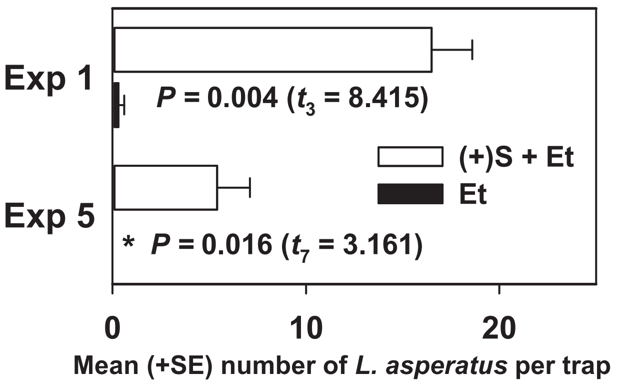

**Fig. 4.** Effects of (+)-sulcatol [(+)S] on catches of *Leptostylus asperatus* in traps baited with ethanol (Et) in experiments 1 (*n* = 67) and 5 (*n* = 43). Treatment with an asterisk had zero catches. *P* = significance level (paired *t* test). *N* = total number caught.

(Madden et al. 1988), the defensive secretions of larval *Gonioctena viminalis* L. (Coleoptera: Chrysomalidae) (Dettner and Schwinger 1987), the pheromone blend produced by male *Phlogophora meticulosa* (L.) (Lepidoptera: Noctuidae) (Aplin and Birch 1970, Birch 1970), and the spacing semiochemical blend for *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae) (Quiroz et al. 1997). Considerable effort is still needed to identify the pheromones and behavioral responses of numerous species of bark and woodboring beetles and their predators, which would help clarify the ecological and evolutionary bases for these patterns.

Bark and woodboring beetles continue to pose threats worldwide as nonnative invasive species (Kirkendall and Faccoli 2010, Haack and Rabaglia 2013, Sweeney et al. 2016, Rassati et al. 2018, Rabaglia et al. 2019). Baited traps are an important component of detection programs for such species (Poland and Rassati 2019, Rabaglia et al. 2019, Rassati et al. 2019). For example, various species of ambrosia beetles from North America such as *G. materiarius* and *M. mali* have been detected in several European countries (Kirkendall and Faccoli

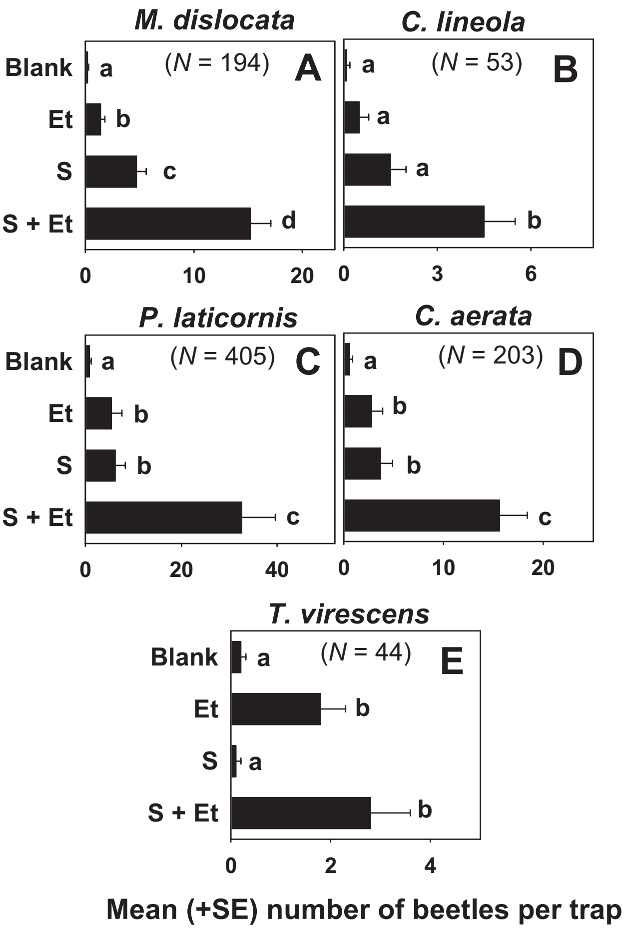

**Fig. 5.** Effects of ethanol (Et) and racemic sulcatol (S) on trap catches of (A) *Madoniella dislocata* ($F_{3,24}$ = 47.75; $P < 0.001$), (B) *Colydium lineola* ($F_{3,24}$ = 9.571; $P < 0.001$), (C) *Pyticeroides laticornis* ($F_{3,24}$ = 24.15; $P < 0.001$), (D) *Coptodera aerata* ($F_{3,24}$ = 26.43; $P < 0.001$), and (E) *Temnoscheila virescens* ($F_{3,24}$ = 12.40; $P < 0.001$) in experiment 6. Means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test). *N* = total number caught.

2010); *G. materiarius* has recently been established in Great Britain (Inward 2020). Although additional experiments would be needed to confirm, a trap lure blend that includes sulcatol may be an effective tool for these species as well as for *M. mutatus*, another recent invader into Italy from South America (Kirkendall and Faccoli 2010) that is considered a serious threat to stands of poplar (*Populus* spp.) worldwide (Alfaro et al. 2007).

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## References Cited

**Alfaro, R. I., L. M. Humble, P. Gonzalez, R. Villaverde, and G. Allegro. 2007.** The threat of the ambrosia beetle *Megaplatypus mutatus* (Chapuis) (=*Platypus mutatus* Chapuis) to world poplar resources. Forestry 80: 471–479.

**Allison, J. D., J. L. McKenney, D. R. Miller, and M. L. Gimmel. 2013.** Kairomonal responses of natural enemies and associates of the southern Ips (Coleoptera: Curculionidae: Scolytinae) to ipsdienol, ipsenol and cis-verbenol. J. Insect Behav. 26: 321–335.

**Aplin, R. T., and M. C. Birch. 1970.** Identification of odorous compounds from male Lepidoptera. Experientia. 26: 1193–1194.

**Birch, M. C. 1970.** Pre-courtship use of abdominal brushes by the nocturnal moth, *Phlogophora meticulosa* (L.) (Lepidoptera: Noctuidae). Anim. Behav. 18: 310–316.

**Borden, J. H. 1982.** Aggregation pheromones, pp. 74–139. *In* J. B. Mitton and K. B. Sturgeon (eds.), Bark beetles in North American conifers. University of Texas Press, Austin, TX.

**Borden, J. H., L. Chong, J. A. McLean, K. N. Slessor, and K. Mori. 1976.** *Gnathotrichus sulcatus*: synergistic response to enantiomers of the aggregation pheromone sulcatol. Science. 192: 894–896.

**Borden, J. H., L. Chong, K. N. Slessor, A. C. Oehlschlager, H. D. Pierce, Jr., and B. S. Lindgren. 1981.** Allelochemic activity of aggregation pheromones between three sympatric species of ambrosia beetles (Coleoptera: Scolytidae). Can. Entomol. 113: 557–563.

**Borden, J. H., J. R. Handley, J. A. McLean, R. M. Silverstein, L. Chong, K. N. Slessor, B. D. Johnston, and H. R. Schuler. 1980a.** Enantiomer-based specificity in pheromone communication by two sympatric *Gnathotrichus* species (Coleoptera: Scolytidae). J. Chem. Ecol. 6: 445–456.

**Borden, J. H., B. S. Lindgren, and L. Chong. 1980b.** Ethanol and α-pinene as synergists for the aggregation pheromones of two *Gnathotrichus* species. Can. J. For. Res. 10: 290–292.

**Borden, J. H., and J. A. McLean. 1979.** Secondary attraction in *Gnathotrichus retusus* and cross-attraction of G. *sulcatus* (Coleoptera: Scolytidae). J. Chem. Ecol. 5: 79–88.

**Byers, J. A. 2007.** Chemical ecology of bark beetles, pp. 89–134. *In* F. Lieutier, K. R. Day, A. Battisti, J. C. Grégoire, and H. F. Evans (eds.), Bark and wood boring insects in living trees in Europe, a synthesis. Springer, The Netherlands.

**Byrne, K. J., A. A. Swigar, R. M. Silverstein, J. H. Borden, and E. Stokkink. 1974.** Sulcatol: population aggregation pheromone in the scolytid beetle, *Gnathotrichus sulcatus*. J. Insect Physiol. 20: 1895–1900.

**Daterman, G. E., and D. L. Overhulser. 2002.** Forest Insect & Disease Leaflet 170. USDA Forest Service, Corvallis, OR.

**Dettner, K., and G. Schwinger. 1987.** Chemical defense in the larvae of the leaf beetle *Gonioctena viminalis* L. (Coleoptera: Chrysomalidae). Experientia 43: 458–460.

**Dodds, K. J., R. P. Hanavan, and M. F. DiGirolomo. 2017.** Firewood collected after a catastrophic wind event: the bark beetle (Scolytinae) and woodborer (Buprestidae, Cerambycidae) community present over a 3-year period. Agric. For. Entomol. 19: 309–320.

**El-Sayed, A. M. 2019.** The Pherobase: database of pheromones and semiochemicals. (http://www.pherobase.com) (accessed 5 December 2019).

**Fletchmann, C. A. H., and C. W. Berisford. 2003.** Identification of sulcatol, a potential pheromone of the ambrosia beetle *Gnathotrichus materiarius* (Col., Scolytidae). J. Appl. Entomol. 127: 189–194.

**Gatti, P., E. Zerba, and P. Gonzalez-Audino. 2011.** Anatomical site of pheromone production and temporal pattern of pheromone emission in the ambrosia beetle *Megaplatypus mutatus*. Physiol. Entomol. 36: 201–207.

**Glantz, S. A. 2005.** Primer of biostatistics, p. 520. McGraw-Hill, New York.

**Gonzalez Audino, P., R. Villaverde, R. Alfaro, and E. Zerba. 2005.** Identification of volatile emissions from *Platypus mutatus* (=sulcatus) (Coleoptera: Platypodidae) and their behavioral activity. J. Econ. Entomol. 98: 1506–1509.

**Haack, R. A., and R. J. Rabaglia. 2013.** Exotic bark and ambrosia beetles in the USA, pp. 48–74. *In* J. Pena (ed.), Potential invasive pests of agricultural crop species. CAB International, Wallingford, United Kingdom.

**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 pheromones of cerambycid beetles; basic science and practical applications. J. Chem Ecol. 42: 631–654.

**Hanks, L. M., J. A. Mongold-Diers, T. H. Atkinson, M. K. Fierke, M. D. Ginzel, E. E. Graham, T. M. Poland, A. B. Richards, M. L. Richardson, and**

**J. G. Millar. 2018**. Blends of pheromones, with and without host plant volatiles, can attract multiple species of cerambycid beetles simultaneously. J. Econ. Entomol. 111: 716–724.

**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.

**Inward, D. J. G. 2020**. Three new species of ambrosia beetles established in Great Britain illustrate unresolved risks from imported wood. J. Pest Sci. 93: 117–126.

**Jordal, B. H., B. B. Normark, and B. D. Farrell. 2000**. Evolutionary radiation of an inbreeding haplodiploid beetle lineage (Curculionidae, Scolytinae). Biol. J. Linn. Soc. 71: 483–499.

**Kirkendall, L. R. 1983**. The evolution of mating systems in bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae). Zool. J. Linn. Soc. 77: 293–352.

**Kirkendall, L. R., and M. Faccoli. 2010**. Bark beetles and pinhole borers (Curculionidae, Scolytinae, Platypodinae) alien to Europe. ZooKeys 56: 227–251.

**Madden, J. L., H. D. Pierce, Jr, J. H. Borden, and A. Butterfield. 1988**. Sites of production and occurrence of volatiles in Douglas-fir beetle, Dendroctonus pseudotsugae hopkins. J. Chem. Ecol. 14: 1305–1317.

**Meier, L. R., J. G. Millar, J. A. Mongold-Diers, and L. M. Hanks. 2019**. (S)-Sulcatol is a pheromone component for two species of cerambycid beetles in the subfamily lamiinae. J. Chem. Ecol. 45: 447–454.

**Meier, L. R., Y. Zou, J. A. Mongold-Diers, J. G. Millar, and L. M. Hanks. 2020**. Pheromone composition and chemical ecology of six species of cerambycid beetles in the subfamily lamiinae. J. Chem. Ecol. 46: 30–39.

**Miller, D. R., C. Asaro, and C. W. Berisford. 2005**. Attraction of southern pine engravers and associated bark beetles (Coleoptera: Scolytidae) to ipsenol, ipsdienol, and lanierone in southeastern United States. J. Econ. Entomol. 98: 2058–2066.

**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, B. F. Barnes, K. J. Gandhi, and D. A. Duerr. 2013**. Attaching lures to multiple-funnel traps targeting saproxylic beetles (Coleoptera) in pine stands: inside or outside funnels? J. Econ. Entomol. 106: 206–214.

**Miller, D. R., C. M. Crowe, K. J. Dodds, L. D. Galligan, P. de Groot, E. R. Hoebeke, A. E. Mayfield, III, 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., K. J. Dodds, A. Eglitis, C. J. Fettig, R. W. Hofstetter, D. W. Langor, A. E. Mayfield, III, A. S. Munson, T. M. Poland, and K. F. Raffa. 2013**. Trap lure blend of pine volatiles and bark beetle pheromones for *Monochamus* spp. (Coleoptera: Cerambycidae) in pine forests of Canada and the United States. J. Econ. Entomol. 106: 1684–1692.

**Miller, D. R., and D. A. Duerr. 2008**. Comparison of arboreal beetle catches in wet and dry cups with Lindgren multiple funnel traps. J. Econ. Entomol. 101: 107–113.

**Millar, J. G., and L. M. Hanks. 2017**. Chemical ecology of cerambycids, pp. 161–208. *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, Y. Zou, C. E. Bográn, M. K. Fierke, M. D. Ginzel, C. W. Johnson, J. R. Meeker, T. M. Poland, *et al*. 2018**. Identifying possible pheromones of cerambycid beetles by field testing known pheromone components in four widely separated regions of the United States. J. Econ. Entomol. 111: 252–259.

**Miller, D. R., and R. J. Rabaglia. 2009**. Ethanol and (-)-alpha-pinene: attractant kairomones for bark and ambrosia beetles in the southeastern US. J. Chem. Ecol. 35: 435–448.

**Pepper, W. D., S. J. Zarnoch, G. L. DeBarr, P. de Groot, and C. D. Tangren. 1997**. Choosing a transformation in analyses of insect counts from contagious distributions with low means. U.S. Dept. Agric.–Forest Service, Res. Pap. SRS-5, Asheville, NC.

**Plummer, E. L., T. E. Stewart, K. Byrne, G. T. Pearce, and R. M. Silverstein. 1976**. Determination of the enantiomeric composition of several insect pheromone alcohols. J. Chem. Ecol. 2: 307–331.

**Poland, T. M., and D. Rassati. 2019**. Improved biosecurity surveillance of non-native forest insects: a review of current methods. J. Pest Sci. 92: 37–49.

**Quiroz, A., J. Pettersson, J. A. Pickett, L. J. Wadhams, and H. M. Niemeyer. 1997**. Semiochemicals mediating spacing behaviour of bird cherry-oat aphid, *Rhopalosiphum padi* feeding on cereals. J. Chem. Ecol. 23: 2599–2607.

**Rabaglia, R. J., A. I. Cognato, E. R. Hoebeke, C. W. Johnson, J. R. Labonte, M. E. Carter, and J. J. Vlach. 2019**. Early detection and rapid response. A 10-year summary of the USDA forest service program of surveillance for non-native bark and ambrosia beetles. Am. Entomol. 65: 29–42.

**Ranger, C. M., A. M. Gorzlancyk, K. M. Addesso, J. B. Oliver, M. E. Reding, P. B. Schultz, and D. W. Held. 2014**. Conophthorin enhances the electroantennogram and field behavioural response of *Xylosandrus germanus* (Coleoptera: Curculionidae) to ethanol. Agric. For. Entomol. 16: 327–334.

**Ranger, C. M., M. E. Reding, P. B. Schultz, J. B. Oliver, S. D. Frank, K. M. Addesso, J. H. Chong, B. Sampson, C. Werle, S. Gill, and C. Krause. 2016**. Biology, ecology, and management of nonnative ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) in ornamental plant nurseries. J. Integr. Pest Mgmt. 7: 9.23.

**Rassati, D., R. A. Haack, M. Knížek, and M. Faccoli. 2018**. National trade can drive range expansion of bark- and wood-boring beetles. J. Econ. Entomol. 111: 260–268.

**Rassati, D., L. Marini, M. Marchioro, P. Rapuzzi, G. Magnani, R. Poloni, F. Di Giovanni, P. Mayo, and J. Sweeney. 2019**. Developing trapping protocols for wood-boring beetles associated with broadleaf trees. J. Pest Sci. 92: 267–279.

**Ray, A. M., E. S. Lacey, and L. M. Hanks. 2006**. Predicted taxonomic patterns in pheromone production by longhorned beetles. Naturwissenschaften. 93: 543–550.

**Ray, A. M., J. G. Millar, J. A. Moreira, J. S. McElfresh, R. F. Mitchell, J. D. Barbour, and L. M. Hanks. 2015**. North American species of cerambycid beetles in the genus neoclytus share a common hydroxyhexanone-hexanediol pheromone structural motif. J. Econ. Entomol. 108: 1860–1868.

**Renwick, J. A. 1977**. Aggregation pheromones in the ambrosia beetle *Platypus flavicornis*. Naturwissenschaften. 64: 226.

**Shore, T. L. 1992**. Ambrosia beetles. Forest Pest Leaflet 72, p. 4. Forestry Canada, Victoria BC.

**Smith, R. H. 2000**. Xylem monoterpenes of pines: distribution, variation, genetics, function. U.S. Dept. Agric.–Forest Service, Gen. Tech. Rep. PSW–GTR–177. Albany, CA.

**Sweeney, J. D., P. Silk, V. Grebennikov, and M. Mandelshtam. 2016**. Efficacy of semiochemical-baited traps for detection of Scolytinae species (Coleoptera: Curculionidae) in the Russian Far East. Eur. J. Entomol. 113: 84–97.

**Turnbow, R. H., and R. T. Franklin. 1980**. Flight activity by Scolytidae in the northeast Georgia Piedmont (Coleoptera). J. Georgia Entomol. Soc. 15: 26–37.

**(USDA) U.S. Department of Agriculture–Forest Service. 1985**. Insects of eastern forests. US Dep. Agric.–Forest Service, Misc. Publ. No. 1426, Washington, D.C.