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Methyl 2,4,6-decatrienoates Attract Stink Bugs and Tachinid Parasitoids

Jeffrey R. Aldrich · Ashot Khrimian · Mary J. Camp

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Abstract *Halyomorpha halys* (Stål) (Pentatomidae), called the brown marmorated stink bug (BMSB), is a newly invasive species in the eastern USA that is rapidly spreading from the original point of establishment in Allentown, PA. In its native range, the BMSB is reportedly attracted to methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate, the male-produced pheromone of another pentatomid common in eastern Asia, *Plautia stali* Scott. In North America, *Thyanta* spp. are the only pentatomids known to produce methyl 2,4,6-decatrienoate [the (*E*,*Z*,*Z*)-isomer] as part of their pheromones. Methyl 2,4,6-decatrienoates were field-tested in Maryland to monitor the spread of the BMSB and to explore the possibility that *Thyanta* spp. are an alternate host for parasitic tachinid flies that use stink bug pheromones as host-finding kairomones. Here we report the first captures of adult and nymph BMSBs in traps baited with methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate in central Maryland and present data verifying that the tachinid, *Euclytia flava* (Townsend), exploits methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate as a kairomone. We also report the unexpected finding that various isomers of methyl 2,4,6-decatrienoate attract *Acrosternum hilare* (Say), although this bug apparently does not produce methyl decatrienoates. Other stink bugs and tachinids native to North America were also attracted to methyl 2,4,6-decatrienoates. These data indicate there are Heteroptera in North America in addition to *Thyanta* spp. that probably use methyl 2,4,6-decatrienoates as pheromones. The evidence that some pentatomids exploit the pheromones of other true bugs as kairomones to find food or to congregate as a passive defense against tachinid parasitism is discussed.

Keywords Aggregation pheromone · Kairomone · Selfish herd · Methyl decadienoate · *Acrosternum* · *Thyanta* · *Podisus* · *Halyomorpha* · *Banasa* · *Euclytia* · *Gymnosoma* · Hemiptera · Heteroptera · Pentatomidae

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Introduction

Much has been learned about stink bug communication, both chemical and acoustic, since *Thyanta custator* (F.) (Pentatomidae) rained from the sky in a line across Kansas on October 14, 1939, requiring truck-loads of bugs to be hauled off in the subsequent cleanup (Wilbur, 1939). It is now known that pentatomid males produce pheromones attractive to conspecific females, males, and nymphs, as well as tachinid flies and other parasitoids (Aldrich, 1988b, 1995; McBrien and Millar, 1999). Ultimately, adult stink bugs recognize and court each other acoustically (Çokl and Virant-Doberley, 2003). Males of *Thyanta* spp., for example, produce methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate with (Millar, 1997; McBrien et al., 2002b) or without particular sesquiterpenes (Moraes et al., 2005) that attract a mate, while at close range, a dialog of substrate vibrations facilitates species recognition and isolation (McBrien et al., 2002a). The methyl 2,4,6-decatrienoate pheromone theme has also been reported for one other pentatomid bug native to eastern Asia, *Plautia stali* Scott, whose males produce methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate (Sugie et al., 1996).

Halyomorpha halys (Stål) (Pentatomidae), called the brown marmorated stink bug (BMSB), is a newly invasive species in the eastern USA (Hoebeke and Carter, 2003) that is rapidly spreading from its original point of establishment in Allentown, PA. The pheromone for *H. halys* is unknown, but in Japan, this bug is reportedly cross attracted to the pheromone of *P. stali* (Tada et al., 2001a, b).

Perhaps the best known pheromone system among the true bugs (Hemiptera: Heteroptera) is that of the spined soldier bug, *Podisus maculiventris* (Say) (Pentatomidae) (Aldrich et al., 1978, 1984a, b, c; Aldrich, 1985; Sant'Ana et al., 1997). Males of this predacious bug produce an attractant pheromone consisting of two essential components, (*E*)-2-hexenal and α-terpineol. Among various parasitoids that exploit this pheromone as a host-finding kairomone, the most commonly encountered species is the tachinid fly, *Euclytia flava* (Townsend). However, *E. flava* is seldom captured in traps baited with synthetic *P. maculiventris* pheromone late in the summer or early fall, and this fly almost never emerges from over wintering spined soldier bugs caught in pheromone-baited traps in the spring. *Euclytia flava* has been reared from *Thyanta* spp. field-collected from late July through September (Eger and Ables, 1981; Jones et al., 1996), suggesting that *Thyanta* bugs might be a late-season alternate host for *E. flava*.

Thus, we became interested in field-testing methyl 2,4,6-decatrienoates for two reasons: (1) in an effort to monitor the spread of the BMSB, *H. halys*, and (2) to explore the possibility that *Thyanta* spp. are an alternate host for the tachinid fly, *E. flava*. Here, we report data pertinent to these two avenues of investigation but also report the unexpected finding that various isomers of methyl 2,4,6-decatrienoate are potent attractants for native stink bugs and their tachinid parasitoids although efforts to isolate these compounds from the bugs themselves have thus far failed.

Methods and Materials

Chemical Standards and Treatments Standards of the following were purchased: (*E*)-2-hexenal, methyl (*E*,*Z*)-2,4-decadienoate (Bedoukian Research, Danbury, CT, USA); α-terpineol (Fisher Scientific, Fair Lawn, NJ, USA); and bisabolene (International Flavors & Fragrances, Union Beach, NJ, USA). Methyl (*E*,*Z*,*Z*)-, (*Z*,*E*,*Z*)-, and (*E*,*E*,*Z*)-2,4,6-decatrienoates were synthesized as previously described (Khrimian, 2005), as were (4*S*)-*cis*- and (4*S*)-*trans*-(*Z*)-α-bisabolene epoxides [(*Z*)-(1*R*,2*S*,4*S*)-4-(1′,5′-dimethyl 1′,4′-hexadienyl)-1, 2-epoxy-1-methylcyclohexane and (*Z*)-(1*S*,2*R*,4*S*)-4-(1′,5′-dimethyl 1′,4′-hexadienyl)-1,2-epoxy-1-methylcyclohexane, respectively] (Chen et al., 2000). Zingiberene [5-(1,5-dimethyl-4-hexenyl)-2-methyl-1,3-cyclohexadiene] was the most convenient sesquiterpene to use for the pheromone because this compound could be isolated from ginger essential oil by using the procedure of Millar (1998). Structures of known pheromone molecules that were tested are shown in Fig. 1.

Lures for the initial experiment (Exp. 1) included treatments mimicking the natural pheromones of *P. maculiventris* (Aldrich et al., 1984a) and *T. custator accerra* McAtee (McBrien et al., 2002b), with five replicates per treatment prepared as follows. (*E*)-2-hexenal and racemic α-terpineol were mixed in a molar ratio of 1:0.843. Batches of 40 ml of pheromone were prepared by combining 17.6 ml hexenal and 21.4 ml of α-terpineol. A 20% (vol/wt) formulation of pheromone in plasticized polyvinyl chloride (PVC) was prepared by mixing 107 g of powdered PVC (Tenneco, Piscataway, NJ, USA) with 53 g of dioctyl phthalate (Aldrich Chemicals, Milwaukee, WI, USA) (Fitzgerald et al., 1973). The

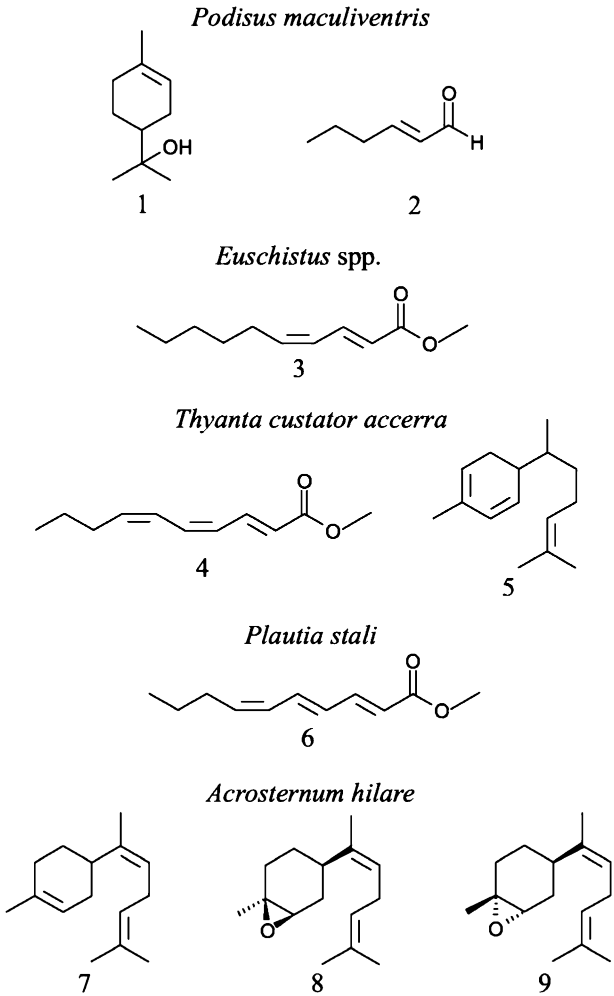

Fig. 1 Chemical compounds tested and the pentatomid species with which the compounds have been associated: *1*, α-terpineol; *2*, (*E*)-2-hexenal; *3*, methyl (*E*,*Z*)-2,4-decadienoate; *4*, methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate; *5*, zingiberene; *6*, methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate; *7*, (*Z*)-α-bisabolene; *8*, *cis*-(*Z*)-α-bisabolene epoxide; and *9*, *trans*-(*Z*)-α-bisabolene epoxide

pheromone–PVC mixture was poured into test tubes (to the top; 16×100 mm, Kimble, Elmira, NY, USA), heated in an oven at 110°C for 30 min, removed from the tubes, and stored in sealed vials in a freezer until use (treatment = "H+α-T"). Approximately 1-g slices of the H+α-T treatment in PVC were used to bait traps.

In Exp. 1, lures for treatments based on the *Thyanta* pheromone were prepared with methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate, designated as "*EZZ*," by placing ten rubber septa (West Pharmaceutical Services, Kearney, NE, USA) in a 100-ml, round-bottom, one-neck flask, and covering the septa with an 8-ml hexane solution containing 40 mg of methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate plus 40 mg of zingiberene. The flask was rotated on a rotary evaporator (without applying a vacuum) for 1.5–2 hr or until the liquid was almost completely absorbed into the septa. One set of septa was placed directly into the bottom of traps unprotected from sunlight; this treatment is defined as "U-*EZZ*+Z." Methyl 2,4,6-decatrienoates undergo photoisomerization when exposed to sunlight (Khrimian, unpublished data); therefore, another set of septa was deployed in traps protected from light by pinning the septa inside ~7-cm-long pieces of standard PVC plumbing pipe (2.5 cm ID); this treatment is coded as "*EZZ*+Z." Analogously, a treatment consisting of methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate (4.4 mg/septum) without zingiberene was prepared (designated "*EZZ*"), and septa impregnated with only hexane served as controls (C).

Lures for a second experiment (Exp. 2) were prepared as described above for the *Thyanta*-based treatments except that a second methyl decatrienoate isomer (the *Z*,*E*,*Z*-isomer) was also used, and the compound previously identified as the main pheromone component of *Euschistus* spp. (Aldrich et al., 1991), methyl (*E*,*Z*)-2,4-decadienoate ("*D*"), was used instead of zingiberene. None of these lures was protected from light. Treatments for Exp. 2 consisted of *EZZ*, *EZZ*+*D*, *D*, *ZEZ*, *EZZ*+*D*, and C, with four replicates per treatment.

On September 10, 2004, three additional treatments (four replicates each) were added to Exp. 2 to test the possibility of an interaction between methyl (*Z*,*E*,*Z*)-2,4,6-decatrienoate and the male-specific compounds previously identified from the green stink bug, *Acrosternum hilare* (Aldrich et al., 1989; McBrien et al., 2001): (*Z*)-α-bisabolene and (4*S*)-*cis*- and (4*S*)-*trans*-(*Z*)-α-bisabolene epoxides. The commercial sample of bisabolene was determined to contain ~20% (*Z*)-α-bisabolene; therefore, septa were loaded with 20 mg of bisabolene so as to contain 4 mg of the desired isomer for one of the additional treatments ("B"), with a second treatment consisting of *ZEZ* (4 mg) + B (10 mg). The third additional treatment consisted of a 1:1 mixture of (4*S*)-*cis*- and (4*S*)-*trans*-(*Z*)-α-bisabolene epoxides ("X"). The amount of epoxides available was limiting (~12 mg); therefore, only one treatment included the epoxides: *ZEZ* (4 mg) + X (3 mg).

Lures for a third experiment (Exp. 3) were prepared by using rubber septa (four replicates per treatment) impregnated with chemicals as described above, except that each septum was loaded with 2-mg active ingredient/lure. Lures were pinned inside PVC pipe as in Exp. 1 and hung from the roof of sticky traps. Treatments consisted of hexane controls (C), methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate (*EEZ*), methyl (*Z*,*E*,*Z*)-2,4,6-decatrienoate (*ZEZ*), and *EEZ*+*ZEZ* (3:1 ratio).

A fourth experiment (Exp. 4) was conducted in 2005 as a follow-up to Exp. 2. Lures were prepared as for Exps. 1 and 2, but methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate was used in place of the (*E*,*Z*,*Z*)-isomer that was part of the Exp. 2 treatment set. Thus, treatments for Exp. 4 consisted of *EEZ*, *EEZ*+*D*, *D*, *ZEZ*, *ZEZ*+*D*, and C, with four replicates per treatment. All treatments for Exp. 4 were protected from light inside PVC pipe as in Exps. 1 and 3. The lures and conditions for the four field trapping experiments are summarized in Table 1.

Table 1 Chemical treatments tested

Exp.	Code	Compound(s)	Formulation	Trap
1	*E*-2H+α-T	(*E*)-2-hexenal +α-terpineol	PVC	Aldrich[a]
1	EZZ_a	Methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate[b]	Septum/protected[c]	Aldrich
1	EZZ_a+*Z*	Methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate + zingiberene	Septum/protected	Aldrich
1	EZZ_b+*Z*	Methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate + zingiberene[d]	Septum/protected	Aldrich
1	U-EZZ_a	Methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate	Septum/unprotected[e]	Aldrich
2	U-*EZZ*[f]	Methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate	Septum/unprotected	Sterling[g]
2	U-*D*	Methyl (*E*,*Z*)-2,4-decadienoate	Septum/unprotected	Sterling
2	U-*EZZ*+*D*	Methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate + methyl (*E*,*Z*)-2,4-decadienoate	Septum/unprotected	Sterling
2	U-*ZEZ*	Methyl (*Z*,*E*,*Z*)-2,4,6-decatrienoate	Septum/unprotected	Sterling
2	U-*ZEZ*+*D*	Methyl (*Z*,*E*,*Z*)-2,4,6-decatrienoate + methyl (*E*,*Z*)-2,4-decadienoate	Septum/unprotected	Sterling
2	U-*ZEZ*+*B*	Methyl (*Z*,*E*,*Z*)-2,4,6-decatrienoate + α-bisabolene	Septum/unprotected	Sterling
2	U-*X*	Bisabolene epoxide	Septum/unprotected	Sterling
2	U-*ZEZ*+*X*	Methyl (*Z*,*E*,*Z*)-2,4,6-decatrienoate + bisabolene epoxide	Septum/unprotected	Sterling
3	*EEZ*	Methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate	Septum[h]	Sticky[I]
3	*ZEZ*	Methyl (*Z*,*E*,*Z*)-2,4,6-decatrienoate	Septum	Sticky
3	*EEZ*+*ZEZ*	Methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate + methyl (*Z*,*E*,*Z*)-2,4,6-decatrienoate	Septum	Sticky
4	*EEZ*	Methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate	Septum/protected	Sterling
4	*D*	Methyl (*E*,*Z*)-2,4-decadienoate	Septum/protected	Sterling
4	*EEZ*+*D*	Methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate + methyl (*E*,*Z*)-2,4-decadienoate	Septum/protected	Sterling
4	*ZEZ*	Methyl (*Z*,*E*,*Z*)-2,4,6-decatrienoate	Septum/protected	Sterling
4	*ZEZ*+*D*	Methyl (*Z*,*E*,*Z*)-2,4,6-decatrienoate + methyl (*E*,*Z*)-2,4-decadienoate	Septum/protected	Sterling

[a] Custom-made clear plastic funnel trap; see text.

[b] First synthetic batch.

[c] Lure pinned inside PVC pipe to shield against sunlight.

[d] Second synthetic batch of methyl (*E,Z,Z*)-2,4,6-decatrienoate.

[e] Unprotected lures (U) were impregnated rubber septa placed in trap bottoms.

[f] Distinction between synthetic batches of methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate was dropped; see text.

[g] Clear plastic funnel trap constructed and supplied by Sterling International.

[h] Lure shielded from direct sunlight by pinning inside trap roof.

[i] Jackson delta traps with removable sticky inserts (Agrisense).

Field Trapping Field experiments were carried out at the USDA Beltsville Agricultural Research Center (BARC), Prince George's County, MD, from June through October of 2004 and August through October of 2005. Experiment 1 was conducted at the South Farm of BARC from June 15 through September 17, 2004, with clear plastic funnel traps designed to capture insects alive (Aldrich et al., 1984a). These traps were hung about 1.8 m above ground from the branches of trees (>20 m apart) in a mixed deciduous forest bordering agricultural fields. Experiment 2 was conducted at the North Farm of BARC from July 1 through October 26, 2004, with traps similar to those used for Exp. 1 supplied by Sterling International (Spokane, WA, USA) and deployed as for Exp. 1. Experiment 3 was conducted from July 9 through October 15, 2004, with Jackson delta traps with removable sticky inserts (Agrisense, Fresno, CA, USA) (Zhang and Aldrich, 2004) deployed along East Line Road at BARC. Experiment 4 was conducted from August 11 through October 19, 2005, with traps located and positioned as in Exp. 2. Traps with the H+α-T treatment were rebaited every 2–3 d; traps with the other treatments on rubber septa were rebaited every 2 wk. Usually traps were monitored daily; insects caught inside, on, and within ~1 m of a trap were counted. Field-collected insects were preserved for species identification and used for further laboratory experimentation.

Statistical Analysis The total numbers of insects responding to the treatments were analyzed with a Fisher's exact Chi-square test by using StatXact (Mehta and Patel, 2003) to determine if the distribution of the insects differed for the chemical compounds. For each species, the treatment counts were analyzed as a multinomial distribution with StatXact. The probabilities that an individual of the particular species would be attracted to the chemical compound were calculated. Confidence intervals were also calculated for the probabilities. If the confidence intervals overlapped for two treatments, then they were not statistically different. The confidence intervals were calculated by using Sidak adjusted *P* values so that the experiment-wise error was 0.05.

Results

Experiment 1 Although treatments containing methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate with or without zingiberene were deployed with the expectation of attracting *Thyanta* spp. pentatomids (McBrien et al., 2002b) and their parasitoids, only six individuals of *T. custator accerra* McAtee [one male and five females (1M:5F)] were captured. In fact, three other stink bug species were more abundantly encountered in or around these traps than was *T. custator accerra* (Fig. 2): *A. hilare* (Say) (5M:11F), *Euschistus tristigmus* (Say) (2M:9F), and *Banasa dimidiata* (Say) (5M:3F). Other pentatomids that were caught included *Euschistus servus* (Say) (2F), *P. maculiventris* (Say) (1M:1F), and *Banasa calva* (Say) (1F). No stink bugs were caught in control traps in Exp. 1.

Five species of tachinid flies were captured in or on traps baited with chemical treatments in Exp. 1: *E. flava* (Townsend), *Gymnosoma par* (Walker), *Euthera tentatrix* Loew, *Hemyda aurata* Robineau–Desvoidy, and *Cylindromyia fumipennis* (Bigot) (Fig. 3).

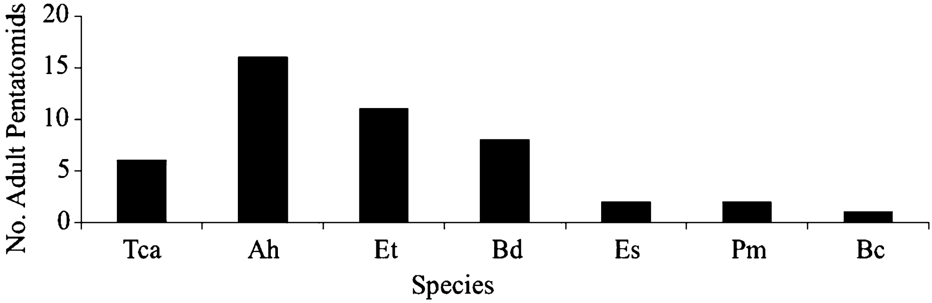

Fig. 2 Adult pentatomid species caught in or around traps baited with lures containing methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate from June 15 through September 17, 2004 (Exp. 1): *Tca*, *T. custator accerra* McAtee; *Ah*, *A. hilare* (Say); *Et*, *E. tristigmus* (Say); *Bd*, *B. dimidiata* (Say); *Es*, *E. servus* (Say); *Pm*, *P. maculiventris* (Say); and *Bc*, *B. calva* (Say)

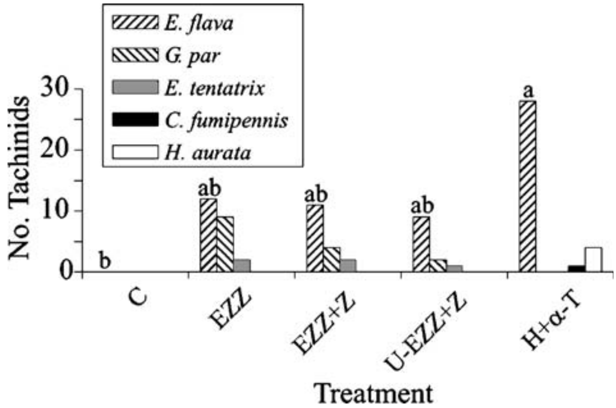

Fig. 3 Tachinid flies caught in or around traps baited with lures containing methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate (*EZZ*) with or without zingiberene (*Z*) [components of *Thyanta* spp. pheromones (McBrien et al., 2002b)], and (*E*)-2-hexenal with α-terpineol [components of the *P. maculiventris* pheromone, H+α-T (Aldrich et al., 1984a)], from June 15 through September 17, 2004 (Exp. 1): *E. flava* (Townsend), *G. par* (Walker), *E. tentatrix* Loew, *H. aurata* Robineau–Desvoidy, and *C. fumipennis* (Bigot). Bars for *E. flava* with different letters are significantly different ($P<0.05$) (trienoate treatments with the prefix "*U*" were unprotected from light; those without a prefix were protected from light as described in the text)

Two of these tachinid parasitoids (*H. aurata* and *C. fumipennis*) were restricted to traps baited with the major pheromone components of the spined soldier bug, *P. maculiventris*, and two other species (*G. par* and *E. tentatrix*) were restricted to traps with treatments containing methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate. The most abundantly encountered species was *E. flava*, and this fly was captured in and around traps containing either methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate or the *P. maculiventris* synthetic pheromone. In the former treatments, the presence or absence of zingiberene did not significantly affect attraction of *E. flava*. No tachinids were caught in or around control traps.

In addition to pentatomids and tachinids, one species of solitary wasp was also attracted in Exp. 1 to treatments containing methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate: *Astata occidentalis* Cresson (Hymenoptera: Sphecidae). A total of seven females were caught inside traps (none in controls) and, as with *E. flava*, the presence of zingiberene appeared not to affect attraction.

Experiment 2 This experiment was designed to further test methyl 2,4,6-decatrienoates by themselves or combined with methyl (*E*,*Z*)-2,4-decadienoate, the previously identified male-specific pheromone component of various *Euschistus* spp. (Aldrich et al., 1991), for attraction of native stink bugs. Methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate was included as an extension of Exp. 1 and methyl (*Z*,*E*,*Z*)-2,4,6-decatrienoate was included based on preliminary gas chromatography–electroantennogram detector data with tachinid flies (Aldrich et al., 2006) and *H. halys* (Zhang and Aldrich, unpublished data).

Substantial numbers of the dusky stink bug, *E. tristigmus*, and the green stink bug, *A. hilare*, were caught during Exp. 2 at chemically treated traps, but none were caught in or around control traps (Fig. 4). For *A. hilare*, almost 38% of the individuals that were attracted were second- to fifth-instar nymphs, and nymphs were often caught in the absence of adults. Methyl (*Z*,*E*,*Z*)-2,4,6-decatrienoate alone was significantly attractive to *A. hilare*, whereas methyl (*E*,*Z*)-2,4-decadienoate alone was not attractive to green stink bugs (Fig. 4a). Methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate alone was more attractive to green stink bugs

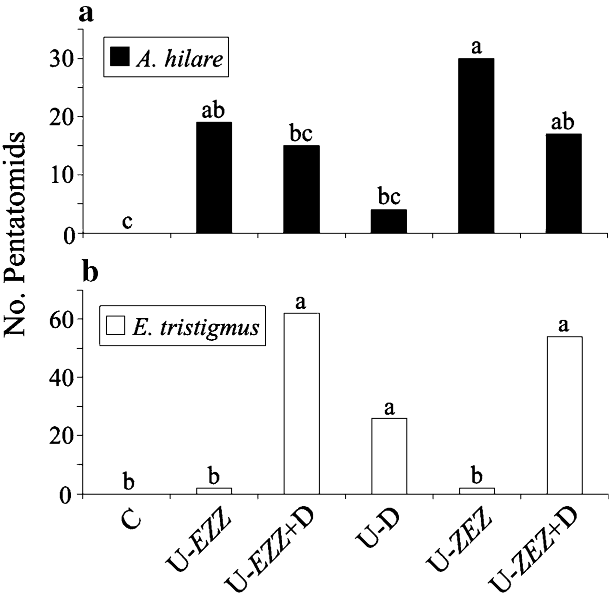

Fig. 4 Total number of pentatomids (adults and nymphs) of **a** the green stink bug, *A. hilare* (Say), and **b** the dusky stink bug, *E. tristigmus* (Say), caught in or around traps baited with lures containing methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate (*EZZ*), methyl (*Z*,*E*,*Z*)-2,4,6-decatrienoate (*ZEZ*), methyl (*E*,*Z*)-2,4-decadienoate (*D*), or the binary combinations *EZZ*+D or *ZEZ*+D from July 1 through October 26, 2004 (Exp. 2). The prefix "*U*" indicates that the lures were unprotected from light. Bars for a species with different letters are significantly different ($P<0.05$)

than control traps, but the number of bugs caught with this decatrienoate isomer was not significantly greater than the number of *A. hilare* captured in and around traps baited with methyl (*E*,*Z*)-2,4-decadienoate alone. Combining either the methyl (*Z*,*E*,*Z*)- or (*E*,*Z*,*Z*)-2,4,6-decatrienoates with methyl (*E*,*Z*)-2,4-decadienoate did not increase attraction over that of the methyl decatrienoates alone (Fig. 4a). More female (33) than male (20) green stink bugs were captured, but this difference was not significant ($X^2=3.19$; $P_{0.05}=3.84$, 1 *df*). No green stink bugs were captured in or around control traps.

For the dusky stink bug, predominantly adults were attracted, with nymphs comprising only about 5% of the *E. tristigmus* individuals caught. Methyl (*E*,*Z*,*Z*)- and (*Z*,*E*,*Z*)-2,4,6-decatrienoates alone were insignificantly attractive to *E. tristigmus*, and the previously known pheromone component [methyl (*E*,*Z*)-2,4-decadienoate] by itself appeared only moderately attractive (Fig. 4b); however, the combination of either methyl (*E*,*Z*,*Z*)- or (*Z*,*E*,*Z*)-2,4,6-decatrienoate with methyl (*E*,*Z*)-2,4-decadienoate did not attract significantly more individuals of *E. tristigmus* than did traps baited with methyl (*E*,*Z*)-2,4-decadienoate alone (Fig. 4b). More *E. tristigmus* females (83) than males (56) were captured ($X^2=5.24$, $P<0.05$). No *E. tristigmus* were caught at control traps.

In Exp. 2, significant numbers of two tachinid species were caught from July 1 through October 26 in or around traps baited with treatments containing methyl (*E*,*Z*,*Z*)- and (*Z*,*E*,*Z*)-2,4,6-decatrienoates, with or without methyl (*E*,*Z*)-2,4-decadienoate: *E. flava* and *G. par* (Fig. 5). *Euclytia flava* was attracted to methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate, but methyl (*E*,*Z*)-2,4-decadienoate was completely unattractive to this fly (Fig. 5a). Methyl (*Z*,*E*,*Z*)-2,4,6-decatrienoate was not attractive to *E. flava* in this experiment, and combining methyl (*E*,*Z*)-2,4-decadienoate with methyl (*E*,*Z*,*Z*)- and (*Z*,*E*,*Z*)-2,4,6-decatrienoate did not increase attraction of *E. flava* over that of these decatrienoates alone. For *G. par* (Fig. 5b), only treatments containing methyl (*E*,*Z*)-2,4-decadienoate were attractive, and the combinations of either methyl (*E*,*Z*,*Z*)- or (*Z*,*E*,*Z*)-2,4,6-decatrienoates with methyl (*E*,*Z*)-2,4-decadienoate were not more attractive than the decadienoate alone. Single specimens of *E. tentatrix* were caught with each chemical treatment, but no tachinids were caught at control traps.

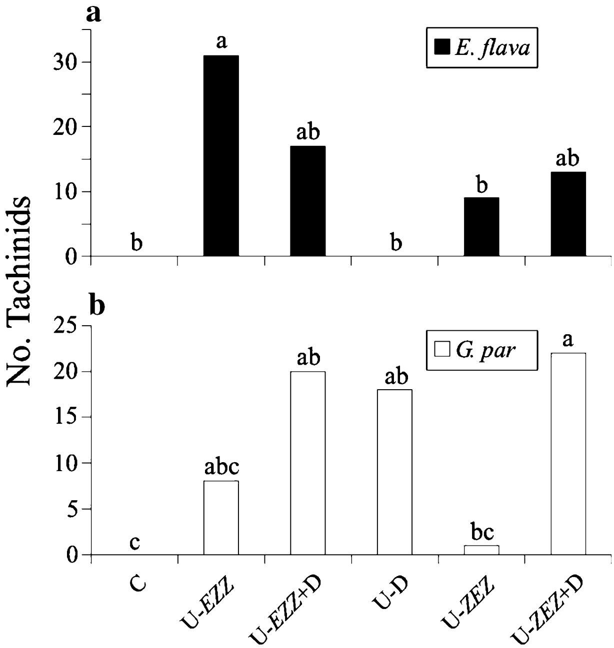

Fig. 5 The tachinid flies, **a** *E. flava* (Townsend) and **b** *G. par* (Walker), caught in or around traps baited with lures containing methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate (*EZZ*), methyl (*Z*,*E*,*Z*)-2,4,6-decatrienoate (*ZEZ*), methyl (*E*,*Z*)-2,4-decadienoate (*D*), or the binary combinations *EZZ*+D or *ZEZ*+D from July 1 through October 26, 2004 (Exp. 2). The prefix "*U*" indicates that the lures were unprotected from light. Bars for a species with different letters are significantly different ($P<0.05$)

Figure 6 shows the numbers of pentatomids (Fig. 6a) and tachinids (Fig. 6b) caught in or around traps for Exp. 2 from September 10 through October 26, 2004, when treatments were added containing (*Z*)-α-bisabolene or (4*S*)-*cis*- and (4*S*)-*trans*-(*Z*)-α-bisabolene epoxides. Treatments containing (*Z*)-α-bisabolene or (*Z*)-α-bisabolene epoxides did not significantly attract either *E. tristigmus* or *A. hilare* (Fig. 6a). Among the tachinids, *Trichopoda pennipes* (F.) was encountered for the first time, but only in the treatment containing methyl (*Z*,*E*,*Z*)-2,4,6-decatrienoate with (4*S*)-*cis*- and (4*S*)-*trans*-(*Z*)-α-bisabolene epoxides (Fig. 6b); 12 individuals of this species (six males and six females) were caught.

Experiment 3 This experiment was conducted to determine if there are native tachinids preadapted to recognize the two methyl decatrienoate isomers thought most likely to attract *H. halys*; i.e., methyl (*E*,*E*,*Z*)- and (*Z*,*E*,*Z*)-2,4,6-decatrienoates. The isomer identified from *P. stali* (Sugie et al., 1996) that is reportedly cross-attractive to *H. halys* in Japan [methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate] (Tada et al., 2001a, b) is, in fact, highly attractive to females of *G. par* (Fig. 7). However, the (*Z*,*E*,*Z*)-isomer was totally unattractive to *G. par*.

Experiment 4 As in Exp. 2, for *A. hilare*, a substantial number of the attracted individuals were nymphs, about 16% of the 127 green stink bugs that were caught. Methyl (*Z*,*E*,*Z*)- and (*E*,*E*,*Z*)-2,4,6-decatrienoate alone were significantly attractive to *A. hilare*, whereas methyl (*E*,*Z*)-2,4-decadienoate alone was not attractive to green stink bugs (Fig. 8a). Combining methyl (*E*,*Z*)-2,4-decadienoate with methyl (*Z*,*E*,*Z*)- or (*E*,*E*,*Z*)-2,4,6-decatrienoates did not increase attraction. The number of females captured (50) was not significantly different than the number of males caught (54). No green stink bugs were captured in or around control traps.

For the dusky stink bug, predominantly adults were attracted, with nymphs comprising about 8% of the *E. tristigmus* individuals caught. Methyl (*E*,*E*,*Z*)- and (*Z*,*E*,*Z*)-2,4,6-decatrienoates alone were insignificantly attractive to *E. tristigmus*. The previously known pheromone component [methyl (*E*,*Z*)-2,4-decadienoate] by itself was attractive (Fig. 8b).

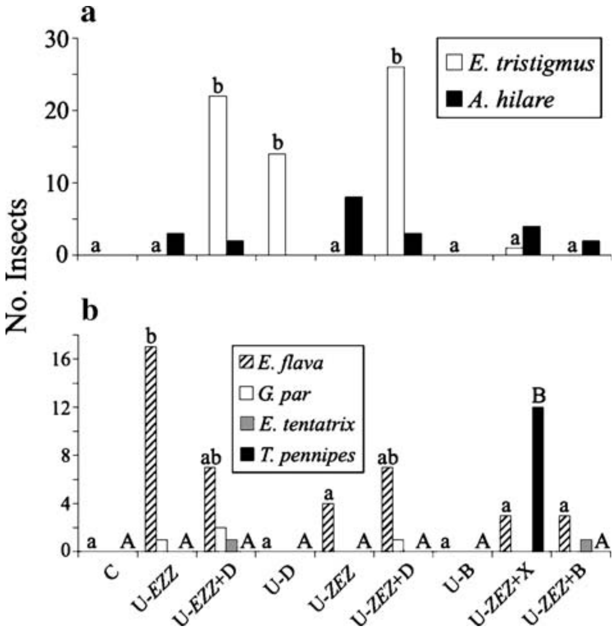

Fig. 6 The total numbers of pentatomids (**a**) and tachinids (**b**) caught in or around traps when treatments containing (*Z*)-α-bisabolene (*B*) or (4*S*)-*cis*- and (4*S*)-*trans*-(*Z*)-α-bisabolene epoxides (*X*) were added to Exp. 2 from September 10 through October 26, 2004 (see text for details). The prefix "*U*" indicates that the lures were unprotected from light. Bars for a species with different letters are significantly different ($P<0.05$)

As in Exp. 2, the addition of methyl 2,4,6-decatrienoates [in this experiment, the (*E*,*E*,*Z*)- and (*Z*,*E*,*Z*)-isomers] to methyl (*E*,*Z*)-2,4-decadienoate did not increase the number of *E. tristigmus* individuals caught relative to traps baited with methyl (*E*,*Z*)-2,4-decadienoate alone (Fig. 8b). In this experiment, the number of *E. tristigmus* females caught (121) was not significantly greater than the number of males captured (108). No *E. tristigmus* were caught at control traps.

Finally, the first captures of the BMSB, *H. halys*, were recorded in Beltsville, MD, during Exp. 4. Three fifth-instar *H. halys* nymphs were caught inside traps baited with methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate on August 15 and 18, and one adult *H. halys* male was captured inside a trap baited with methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate plus methyl (*E*,*Z*)-2,4-decadienoate on September 1, 2005. The cuticle of the adult male was soft and pale in coloration, suggesting it recently eclosed to adult.

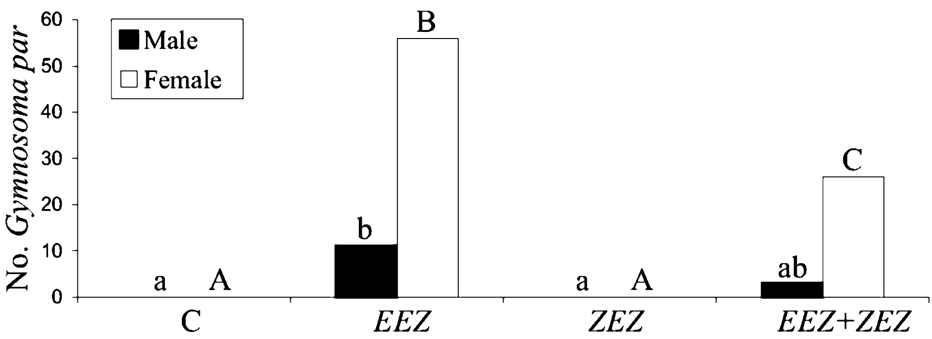

Fig. 7 The total number of *G. par* (Walker) caught in sticky traps baited with methyl (*E*,*E*,*Z*)- and/or (*Z*,*E*,*Z*)-2,4,6-decatrienoate (*EEZ* and *ZEZ*) from July 9 through October 15, 2004. Bars for a species with different letters are significantly different ($P<0.05$)

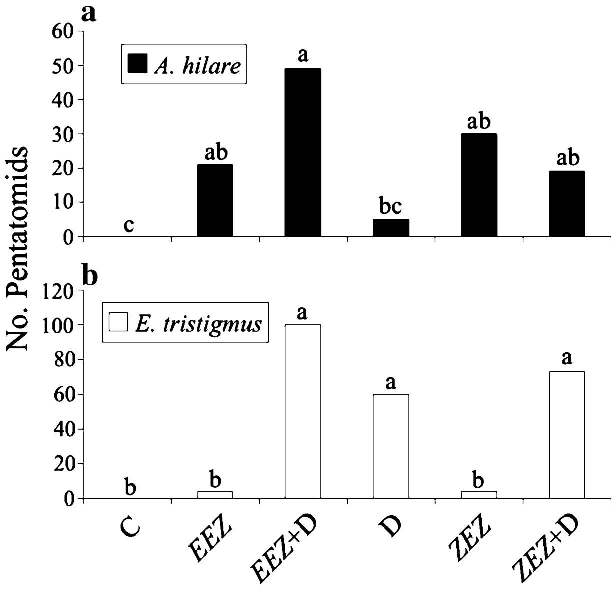

Fig. 8 The total number of pentatomids (adults and nymphs) of **a** the green stink bug, *A. hilare* (Say), and **b** the dusky stink bug, *E. tristigmus* (Say) caught in or around traps baited with lures containing methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate (*EEZ*), methyl (*Z*,*E*,*Z*)-2,4,6-decatrienoate (*ZEZ*), methyl (*E*,*Z*)-2,4-decadienoate (*D*), or the binary combinations *EEZ*+D or *ZEZ*+D from August 11 through October 19, 2005 (Exp. 4). Bars for a species with different letters are significantly different ($P<0.05$)

Discussion

Results presented herein, along with data from field tests conducted near Allentown, PA (Khrimian et al., 2006), verify that the BMSB, *H. halys* (Stål) (Pentatomidae) is, indeed, attracted to methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate (Tada et al., 2001a, b) and related geometric isomers. In addition, tests of synthetic pheromone for *T. custator accerra* McAtee show that the tachinid fly parasitoid, *E. flava* (Townsend), does use the pheromone of *Thyanta* as a host-finding kairomone. However, the most surprising result from our field research is the discovery that other native stink bugs and tachinids are also attracted to methyl 2,4,6-decatrienoates.

Two species, in particular, were significantly attracted to certain methyl 2,4,6-decatrienoates: the green stink bug, *A. hilare* (Say), and the tachinid fly, *G. par* (Walker). Each of these species is native to North America, yet what is known of their chemical ecology raises more questions than answers as to why they are attracted to methyl decatrienoates.

Gymnosoma spp. are known parasitoids of *Euschistus* stink bugs (Arnaud Jr., 1978; Aldrich, 1995) but do not normally parasitize *A. hilare* (see also: Eger and Ables, 1981; Jones et al., 1996). We found that *G. par* females are attracted to methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate, the methyl decatrienoate isomer seemingly most attractive to the BMSB, suggesting to us that this fly might be preadapted to recognize *H. halys* in the USA. In fact, field-collected *G. par* caged in the laboratory with *H. halys* adults did profusely oviposit on the bugs (exclusively underneath the wings) (Aldrich et al., 2006). However, examination of several hundred wild BMSB adults from Allentown failed to reveal any eggs underneath the wings of these bugs. On the other hand, two *T. pennipes* (F.) were reared from field-collected *H. halys* adults (Aldrich et al., 2006); *T. pennipes* is the only known tachinid parasitoid of *A. hilare* in North America (Arnaud Jr., 1978). While *G. par* was highly attracted to methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate, this fly was totally indifferent to the (*Z*,*E*,*Z*)-isomer. The fact that this abundant North American tachinid parasitoid of pentatomids is so finely tuned to a compound yet to be found from any native heteropteran is probably an indication of our semiochemical ignorance; there must be other bugs in North America that produce methyl decatrienoates as part of their attractant pheromones.

A clue as to which pentatomid species might be producing methyl 2,4,6-decatrienoates as pheromone components comes from prey records of the solitary wasp, *A. occidentalis* Cresson (Sphecidae). Females of this sphecid use methyl (*E*,*Z*,*Z*)-2,4,6-decatrienoate as a kairomone to find *Thyanta* adults with which to provision their nests (Millar et al., 2001, and data presented herein). In addition to *Thyanta* spp., Evans (1957) lists *Hymenarcys nervosa* (Say) (Pentatomidae) as the most abundant prey of *A. occidentalis* in Indiana, and also recorded *B. calva* (Say) (Pentatomidae) as prey. Notably, in our 2004 test of synthetic *T. custator accerra* pheromone, more individuals of *B. dimidiata* (Say) were attracted than *Thyanta*, and one individual of *B. calva* was captured.

Why are nymphs and adults of the green stink bug, *A. hilare*, attracted to methyl 2,4,6-decatrienoates? Male-specific volatiles identified from *A. hilare* include straight-chain hydrocarbons, a cyclic sesquiterpene [(*Z*)-α-bisabolene], and *cis*- and *trans*-(*Z*)-α-bisabolene epoxides (Aldrich et al., 1989, 1993); compounds quite unlike methyl decatrienoates. McBrien et al. (2001) reinvestigated the suspected pheromone chemistry of *A. hilare*, demonstrating that females are significantly attracted to a blend of synthetic (*Z*)-α-bisabolene epoxides mimicking the natural blend, but methyl decatrienoates were not among the volatiles isolated from *A. hilare* in this study either, nor are there records of these types of methyl esters from plants. To our knowledge, the most closely related known phytochemicals are 2,4,6-decatrienoic acids from certain *Euphorbia* spp. (Warnaar, 1977, 1981), plants unlikely to be hosts of any of the stink bugs in question here (McPherson, 1982).

If the only natural sources of methyl decatrienoates are *Thyanta* and some other yet-to-be-discovered species of bugs, then one possible explanation for the observed attraction of *A. hilare* to these esters is that green stink bugs are cross-attracted to the pheromones of these other bugs. How plausible an explanation is this? Certainly the most clear-cut examples of heteropterans exploiting the signals of other species are cases involving predation, such as kairomonal attraction of predacious anthocorid bugs to sex pheromones of pine bast scales (Hemiptera: Matsucoccidae) (Mendel et al., 2004), and chemicals (Yasuda, 2000), or even vibrations (Pfannenstiel et al., 1995), associated with the prey of predacious pentatomids. A convincing case of cross-attraction between heteropterans within the same trophic level, however, has recently been reported by Endo et al. (2006). While investigating a complex of bugs that are pests of soybean in Japan, these authors found that the pentatomid, *Piezodorus hybneri* (Gmelin), is significantly attracted to a pheromone component of a competitor, *Riptortus clavatus* (Thunberg) (Heteroptera: Alydidae). These two species have no pheromone compounds in common, nor do soybean plants produce the cross-attractive compound. Endo et al. (2006) speculated that *P. hybneri* utilizes the aggregation pheromone of *R. clavatus* as a kairomone to search for food plants. In fact, the reported cross-attraction of *H. halys* to the pheromone of *P. stali* [i.e., methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate] (Tada et al., 2001a, b) may be another example of such a kairomone.

Acrosternum hilare has a distinct preference for certain native hosts, mainly wild bushes and trees, and a succession of hosts appears to be necessary to sustain a population (Schoene, 1933). Cultivated crops are usually damaged only when the wild-host succession is broken. Given this phenology, it may be adaptive for green stink bug adults and nymphs to go to the pheromones of congeneric bugs in the habitat. The fact that pentatomid nymphs, even young nymphs, are often attracted to the pheromones of conspecific males (Aldrich, 1988a, 1995) supports the idea that pheromones may be associated with food because nymphs are obviously not seeking a mate.

Aside from finding food or a mate, another possible advantage of gregariousness for animals is defense, due to the so-called selfish herd effect, whereby the probability of an individual being attacked by a predator decreases (is diluted) the larger the group (Hamilton, 1971). The concept is relevant not just in cases of predation but also as a passive means of defense against parasites (Mooring and Hart, 1992) and parasitoids (Wcislo, 1984) and applies to mixed species aggregations as well (Hamilton, 1971; Watt and Chapman, 1998; Gibson et al., 2002; Pereira et al., 2004).

The extent to which tachinid parasitoids cue on heteropteran semiochemicals to find these hosts is striking (Aldrich, 1995; Aldrich and Zhang, 2002; Aldrich et al., 2006). Ironically, the stink gland secretions of stink bugs are, by and large, ineffective against tachinids, and the allomones of bugs are even occasionally usurped as kairomones by these flies (Aldrich, 1995). Early tests of the aggregation pheromone for the predatory spined soldier bug, *P. maculiventris* (Say) (Pentatomidae), demonstrated that the bugs avoid entering traps on which tachinid parasitoids are perched (Aldrich et al., 1984a). Thus, tachinids probably have been and continue to be a major selective agent of Heteroptera. Most tachinid parasitoids of Heteroptera belong to the subfamily Phasiinae, which lay a single macrotype egg on a host with only one tachinid larva able to develop per host. Phasiines do not scent-mark their hosts and seem unable to recognize the presence of other eggs on a bug (Stireman et al., 2006); therefore, when these flies are confined in cages with potential hosts, they usually oviposit repeatedly on the same bugs (Aldrich et al., 2006). It is unlikely that this is how phasiines behave in nature. One can imagine that these flies search for a potential host, oviposit on one host whether it is part of an aggregation or solitary, and then fly off to find another host patch. If this scenario is accurate, then the common gregarious behavior of bugs may represent a selfish herd passive defense against tachinid parasitism. Interestingly, mixed aggregations of *H. halys* and *A. hilare* nymphs have occasionally been seen in the field near Allentown, PA (Gary Bernon, USDA-APHIS, personal communication).

Despite the mystery of why various heteropterans and their parasitoids are attracted to methyl decatrienoates, the discovery that these compounds are attractive to economically important bugs may provide another useful semiochemical tool for monitoring and management (e.g., Cullen and Zalom, 2005). This is especially important now that there is a resurgence of problems with bugs because of their immunity to the Bt endotoxin in genetically modified crops (Millar et al., 2002).

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