Synergistic Chemical Attraction of the Eastern Yellowjacket, *Vespula maculifrons* (Hymenoptera: Vespidae)[1]

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Abstract Combinations of (*E*)-2-hexenal diethyl acetal, racemic α-terpineol or linalool, with or without benzyl alcohol incorporated into polyvinyl chloride attracted wasps in the *Vespula vulgaris* species group, including the Eastern, *Vespula maculifrons* (Buysson), and German, *V. germanica* (F.), yellowjackets. (*E*)-2-Hexenal diethyl acetal degrades to release (*E*)-2-hexenal (the active attractant form) and ethanol, which may help kill yellowjackets caught in the water inside the traps used for testing. Combining the (*E*)-2-hexenal diethyl acetal/α-terpineol or linalool mixtures with another blend previously reported as attractive to yellowjackets (acetic acid/isobutanol) synergistically attracted the Eastern yellowjacket. It is hypothesized that the synergistic attraction is a result of combining volatile chemicals associated with carbohydrate feeding (acetic acid/isobutanol) and volatiles associated with foraging for insect prey (hexenal/α-terpineol or linalool).

Key Words yellow jacket, Vespinae, tritrophic, semiochemistry, leaf aldehyde, foraging behavior

Yellowjackets—eusocial wasps in the genera *Vespula* Thomson and *Dolichovespula* Rohwer (Hymenoptera: Vespidae: Vespidae)—differ fundamentally from bees (with which they are often confused by the public) in that they must obtain meat in the form of arthropod prey or scavenged flesh to rear their brood (Akre et al. 1981). Carbohydrate-rich foods such as nectar, sap, and fruit are also sought by yellowjackets as energy sources (Richter 2000). Learning is likely involved to some extent in responses of wasps to odors associated with natural sources of carbohydrates and proteins (Jander 1998).

Members of the *V. vulgaris* species group include the yellowjackets most often a stinging hazard to humans because they produce large colonies whose workers have a propensity to scavenge for protein at picnics, garbage cans and the like; whereas, members of the *V. rufa* group are less often a threat to humans because they have smaller colonies and scavenge only for live prey (Akre et al. 1981). Foremost among species that are dangerous to man are the Eastern yellowjacket, *V. maculifrons* (Buysson); the German yellowjacket, *V. germanica* (F.); and the Western yellowjacket, *V. pensylvanica* (Saussure).

In 1962, while field-testing attractants for flies, Davis et al. (1967) discovered that

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2,4-hexadienyl butyrate was powerfully attractive to *V. pensylvanica*. Subsequent tests showed that the simple saturated ester, heptyl butyrate, was as attractive to the Western yellowjacket as was 2,4-hexadienyl butyrate (Davis et al. 1969), and heptyl butyrate is to this day the best commercially available attractant (Sterling International Inc., Spokane, WA) for the Western yellowjacket (Landolt et al. 2003). However, heptyl butyrate is ineffective for attraction of yellowjackets occurring in the eastern United States (Grothaus et al. 1973, Howell et al. 1974, Reed and Landolt 2002), including the German yellowjacket (Spurr 1996).

Aldrich et al. (1985, 1986) reported the first chemical blends specifically but only moderately attractive to nuisance species of yellowjackets in the eastern U.S.; (*E*)-2-hexenal (leaf aldehyde) acts synergistically with either linalool or α-terpineol to attract members of the *V. vulgaris* group. More recently Landolt (1998) noticed that yellowjackets were attracted to fermented molasses and, based on this observation, he determined that the combination of acetic acid and isobutanol (2-methyl-1-propanol) attracted *V. pensylvanica* and *V. germanica* in tests conducted in the state of Washington. Later, Landolt et al. (1999, 2000) demonstrated that the acetic acid/isobutanol blend is attractive to the Eastern yellowjacket, *V. maculifrons,* plus various other yellowjacket and paper wasps (Vespinae: *Polistes* spp.) (Reed and Landolt 2002). Day and Jeanne (2001) verified that *V. maculifrons* workers are attracted to acetic acid/isobutanol, showed that drones are attracted to this blend as well, and found that *V. vidua* (Saussure) (a member of the *V. rufa* species group) is specifically attracted to ethyl (*E,Z*)-2,4-decadienoate (the "pear ester") concluding, "that the search for strong attractants may be furthered by experimenting with combinations of compounds."

The present investigation was undertaken (1) to optimize formulations of (*E*)-2-hexenal-based synergistic blends for yellowjacket attraction and, (2) to determine if the combination of hexenal-based synergistic blends with the acetic acid/isobutanol synergistic blend would further increase yellowjacket attraction. Also, the role of benzyl alcohol, a major component of the stink bug pheromone (Aldrich et al. 1985) to which yellowjackets were first noticed to be attracted, was reinvestigated with regard to yellowjacket attraction.

Materials and Methods

Preparation of lures. Synthetic compounds formulated in polyvinyl chloride (PVC; Tenneco, Piscataway, NJ) for testing were purchased as follows: (*E*)-2-hexenal and (*E*)-2-hexenal diethyl acetal (Bedoukian Research Inc., Danbury, CT); racemic α-terpineol (α,α,4-trimethyl-3-cyclohenene-1-methanol; *p*-menth-1-en-8-ol) (Fisher Scientific Company, Fair Lawn, NJ); racemic linalool (3,7-dimethyl-1,6-octadien-3-ol), heptyl butyrate, and benzyl alcohol (Aldrich Chemicals, Milwaukee, WI).

PVC plugs containing volatiles were prepared after the method of Fitzgerald et al. (1973) as follows (using the (*E*)-2-hexenal diethyl acetal (=A)/linalool (=L) as an example): PVC resin (200 g) was mixed thoroughly with 60 ml of dioctyl phthalate (Aldrich Chemicals), a blend of 30 ml of A with 20 ml of L was poured into the plasticized PVC and mixed, the material was then poured into test tubes (entirely filling the tubes), and heated at 110°C for 30 min. This processing resulted in sufficient expansion of the material to be able to remove the plasticized PVC plug from the tube. A 5-cm long piece of PVC plug (approximately 5 g) was used to bait traps as described below. PVC plugs containing A + α-terpineol (=T) (=A/T) were prepared

similarly. Plugs including benzyl alcohol (=B) (A/T/B and A/L/B) were prepared as for A/L and A/T, but with an additional 100 µl of B. PVC plugs of (*E*)-2-hexenal (=H) + α-terpineol (=T) (=H/T) or L (=H/L) were prepared with 20 ml of each compound (a lower amount of H being used to account for the difference in molecular weight from A); plugs including B (H/T/B and H/L/B) were prepared as for the latter blends, but with an additional 100 µl of B. The PVC plug for heptyl butyrate (=HB) was made using 20 ml of HB.

The acetic acid/isobutanol lures (AA/IB) were prepared by Sterling International, Inc., Spokane, WA, in a proprietary manner by treating a crystalline acetate salt with isobutanol, and wrapping this mixture in a water soluble plastic-like material. A pouch prepared in this manner was contained inside a sealed Rescue Disposable Yellowjacket Trap® (Sterling International) until use.

Chemical analysis. Release of volatiles from an A/L/B-PVC plug was checked using solid-phase microextraction (SPME; 100 µm polydimethylsiloxane-coated fiber, Supelco Inc., Bellefonte, PA). The plug was first placed in a 1-liter glass jar with a Teflon-lined top having a hole just big enough to insert the SPME needle. The SPME fiber was conditioned in the injector port (260°C) of a Hewlett Packard 6890 gas chromatograph (GC) for 5 min, the needle was then inserted into the top of the jar, and the fiber was extruded for an exposure period of 15 sec (a time determined by trial and error to not overload the fiber). The fiber was then desorbed for 2 min in the GC injector onto a 60 m × 0.25-mm ID, 0.25-mm film-thickness DB-WAXetr capillary column (J&W Scientific Inc., Folsom, CA) in the splitless mode with nitrogen as carrier (2 ml/min) beginning at 50°C for 2 min, then programmed to 250°C at 15°C/min, using flame ionization detection. After the initial headspace sampling, 400 ml of tap water and 1 ml of acetic acid were added to the jar, the volatiles in the headspace over the acidified water containing the A/L/B-PVC plug were sampled as above using a 30 min exposure of the fiber, and analyzed by GC as above. Finally, the fiber was exposed in the acidified water containing the A/L/B-PVC plug for 30 min, and analyzed by GC.

Samples prepared as described were also analyzed by gas chromatography-mass spectrometry on an HP 6890 GC coupled to an HP 5973 Mass Selective Detector using the same type of GC column and conditions as listed above except with helium as carrier gas. Identifications based on mass spectrometry were verified by chromatographic comparison to the known standards.

Field testing. At the start of a test, each Rescue Disposable Yellowjacket Trap® was unsealed to allow extension of the top entrance baffle, and approximately 500 ml of tap water was added to each trap. Addition of water quickly dissolved the pouch, initiating release of acetic acid and isobutanol. PVC plugs containing the various treatments were added by cutting a slit in the top of the plastic bag trap, dropping the piece of volatile-impregnated PVC into the water, and sealing the slit with a piece of tape. Control traps (2000 experiments) were filled with water, but lacked AA/IB pouches or other treatments.

Traps were hung from trees or fences 1.5 to 2 m from the ground at three locations: (1) Beltsville Agricultural Research Center-West (BARC) (1998 and 2000), (2) University of Maryland apiary (College Park campus, 1998) and, (3) a private residence with apple trees in the backyard (1314 Crockett Lane, Silver Spring, MD, 2000). For the experiments at BARC, traps were hung from the branches of deciduous or coniferous trees on the edge of a small woodlot (approximately 1 ha) bordering an urban area of houses, apartments, and a small shopping center (including a bakery). The traps were deployed in groups consisting of 1 trap per each treatment

with the traps spaced approximately 3 m apart in a group; the groups were separated by approximately 10 m. The dates and replications for tests at BARC are listed in the figure legends, and these traps were monitored and rebaited weekly. Traps at the private residence were hung singly from small trees in the backyard; 2 replicates per treatment (A/L/B, IB/AA, IB/AA+A/L/B, and unbaited controls) from 8 to 18 September. Traps at the UMD apiary were hung singly from tree branches around the property; 1 replicate per treatment (A/T/B, H/T/B, IB/AA, IB/AA+A/T/B, IB/AA+H/T/B, and an unbaited control) from 23-30 September. After exposure in the field as indicated, traps were brought to the laboratory to sort and count insects by species.

Statistical analyses. Field-trapping data for locations 1 and 2 above were transformed by $\log(x + 1)$ to correct for non-normality and heteroscedasticity, and then subjected to analysis of variance (ANOVA), followed by the Ryan-Einot-Gabriel-Welsch (REGWQ) multiple range test (SPSS 10.1 for Windows) to separate means (Day and Quinn 1989). The total captures in location 3 were compared by the Chi-square goodness of fit test at $\alpha = 0.05$.

Results

Chemical analyses. The headspace analyses for the A/L/B-PVC plug alone showed that relatively small amounts of ethanol **(1)** and (*E*)-2-hexenal **(2)** were released (5 and 14%, respectively), with greater amounts of (*E*)-2-hexenal diethyl acetal (**3;** 44%) and linalool (**4;** 28%), and traces (<1%) of several impurities as well as benzyl alcohol (**5;** 0.3%) (Fig. 1A). After addition of acidified water, headspace volatiles consisted of (*E*)-2-hexenal (35%), linalool (61%), benzyl alcohol (1%), and traces of impurities; ethanol and (*E*)-2-hexenal diethyl acetal were undetectable (Fig. 1B). GC analysis of the SPME fiber immersed in the acidified water with the A/L/B-PVC plug revealed only (*E*)-2-hexenal (24%) and linalool (75%) (Fig. 1C).

1998 tests. The experiment conducted from 17 to 23 September at BARC (Fig. 2) verified for *V. maculifrons* that (*E*)-2-hexenal diethyl acetal could effectively be used to generate (*E*)-2-hexenal (capture with H/T/B was not significantly different from that with A/T/B), and suggested a trend toward synergism of (*E*)-2-hexenal-based lures by AA/IB. In a separate test conducted from 18 to 24 September at the University of Maryland apiary testing the same lures as for the data presented in Fig. 2 (N = 2), a total of 6 honeybees were captured compared to 42 workers of *Vespula* spp. (Chi-square = 33.33, $P < 0.005$); the Southern yellowjacket, *V. squamosa* (Drury), was the most abundant yellowjacket species at this site (32), followed by *V. maculifrons* (9) and *V. germanica* (1). For the *V. squamosa* caught at the apiary site, the number of wasps attracted to H/T/B and A/T/B did not differ from the unbaited control trap (Chi-square = 2.00; $P_{0.05} = 5.99$), whereas attraction to AA/IB was significantly greater than to H/T/B or A/T/B (Chi-square = 28.30, $P < 0.005$); however, at this site attraction to AA/IB did not differ significantly from that to AA/IB+H/T/B or AA/IB+A/T/B (Chi-square = 3.30; $P_{0.05} = 5.99$).

The experiment from 23 September to 1 October (Fig. 3) at the same BARC location as for the earlier experiment indicated for *V. maculifrons* that (1) linalool could effectively replace α-terpineol (capture with AA/IB+A/T was not significantly different from that for AA/IB+A/L), (2) benzyl alcohol was not necessary for attraction (capture with AA/IB+A/T/B was not significantly greater than that for AA/IB+A/T) and, (3) that AA/IB does synergize attraction to (*E*)-2-hexenal-based lures (capture with AA/IB+A/T, AA/IB+A/L or AA/IB+A/T/B were significantly greater than that of either AA/IB or A/L

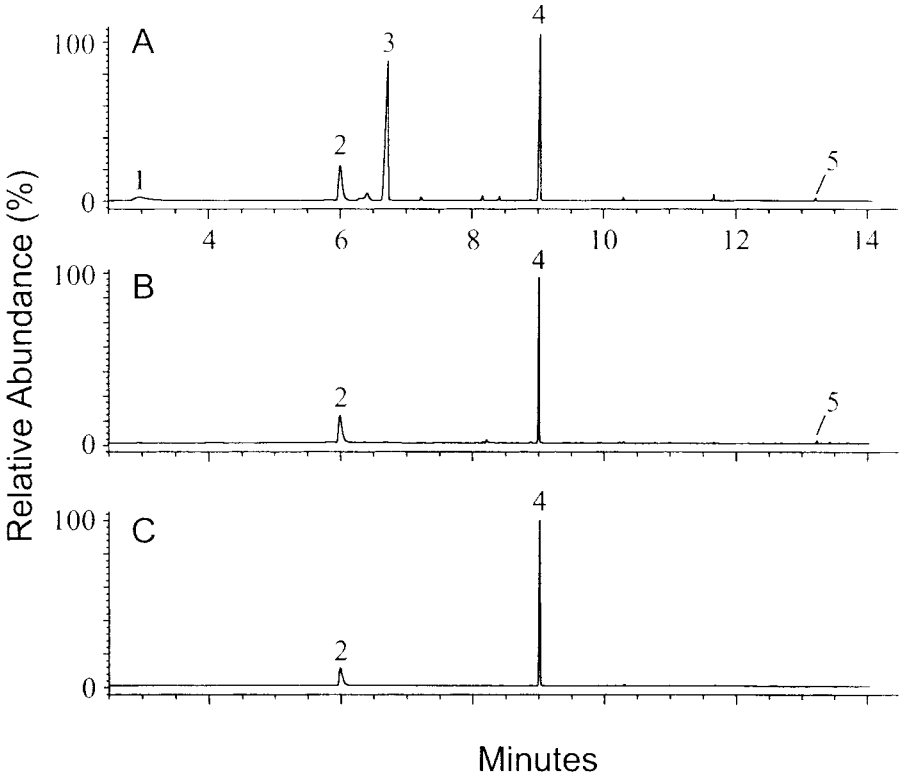

Fig. 1. Solid-phase microextraction (SPME) analyses of a polyvinyl chloride lure containing a blend of (*E*)-2-hexenal diethyl acetal **(3),** linalool **(4)** and benzyl alcohol **(5)** (3:2:0.1, respectively) (**1** = ethanol, **2** = (*E*)-2-hexenal; other details in text). (A) Gas chromatographic (GC) analysis of headspace from lure without water added. (B) GC analysis of headspace for lure with acidified water added. (C) GC analysis of compounds adsorbed onto the SPME fiber immersed in the acidified water containing the lure.

alone or their summation). The interaction between heptyl butyrate and (*E*)-2-hexenal-based lures was equivocal as capture of *V. maculifrons* in traps baited with HB+A/T/B was not significantly greater than that for traps baited with A/L alone, but also was not significantly less than captures for traps baited with AA/IB+A/T, AA/IB+A/L or AA/IB+A/T/B (Fig. 3), nor were HB and A/T/B included as single treatments.

2000 tests. One experiment was conducted continuously from 10 August to 12 October to test for synergism between AA/IB and A/L/B (Fig. 4). In this experiment spanning the peak of *V. maculifrons* activity, AA/IB+A/L/B exhibited a clear synergism over the AA/IB or A/L/B lures tested alone, and the individual lures, while not differing from each other in attractiveness to Eastern yellowjacket workers, were each significantly more attractive to *V. maculifrons* than unbaited control traps.

Table 1 shows data collected with traps deployed at a private residence in Silver

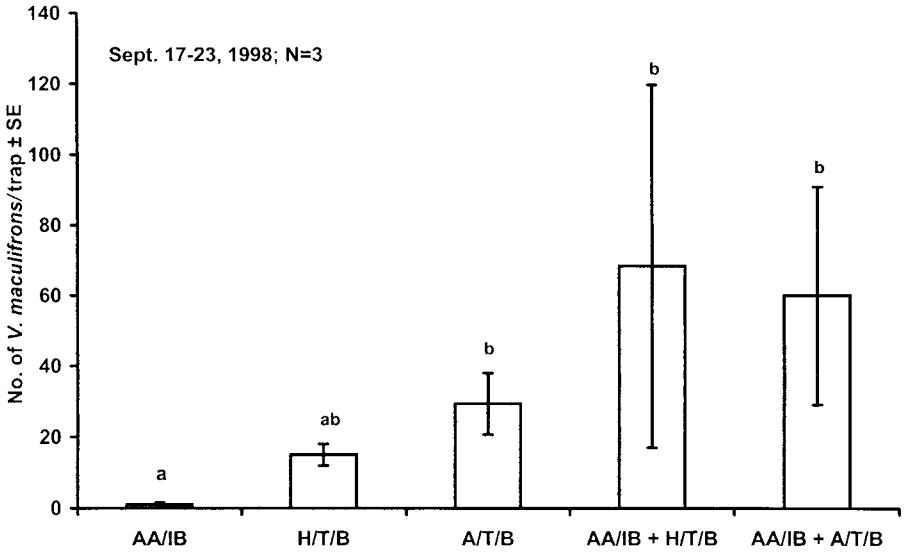

Fig. 2. Mean number of *Vespula maculifrons* workers (±SE; n = 3) caught from September 17-23, 1998, in traps baited with acetic acid/isobutanol (AA/IB) and/or (*E*)-2-hexenal/monoterpenol-based lures (H = (*E*)-2-hexenal, T = α-terpineol, B = benzyl alcohol, A = (*E*)-2-hexenal diethyl acetal). Means followed by the same letter are not significantly different ($P > 0.05$).

Spring, MD, from 8 to 18 September in an area rich in *Vespula* and *Polistes* spp. *Vespula germanica* appeared to be the dominant yellowjacket species in the vicinity, and the data indicate that German yellowjacket workers are synergistically attracted to the combination of AA/IB+A/L/B. These data also again show that *V. maculifrons* workers are synergistically attracted to AA/IB+A/L/B and, at this site, this synergism was indicated for workers of the hybrid yellowjacket (*V. flavopilosa* Jacobson) and the Southern yellowjacket, *V. squamosa.* The invasive species, *Polistes dominulus* (Christ), was the most commonly collected paper wasp, and this species was significantly attracted only to AA/IB+A/L/B (Table 1).

Discussion

Early research on yellowjacket chemical attraction showed that single compounds, such as heptyl butyrate or related esters, are highly attractive to *Vespula pensylvanica* (Davis et al. 1967, Davis et al. 1968, Davis et al. 1969). The first indication that combinations of simple volatile compounds (by themselves inactive) could act synergistically to attract yellowjackets was the discovery that members of the pestiferous *V. vulgaris* species group are attracted to combinations of leaf aldehyde, (*E*)-2-hexenal, with either of the common plant monoterpenols, linalool or α-terpineol (Aldrich et al. 1985, Aldrich et al. 1986). More recent experiments have shown that acetic acid synergizes the attraction of various yellowjackets and paper wasps to isobutanol, heptyl butyrate, and butyl butyrate (Day and Jeanne 2001, Reed and Landolt 2002).

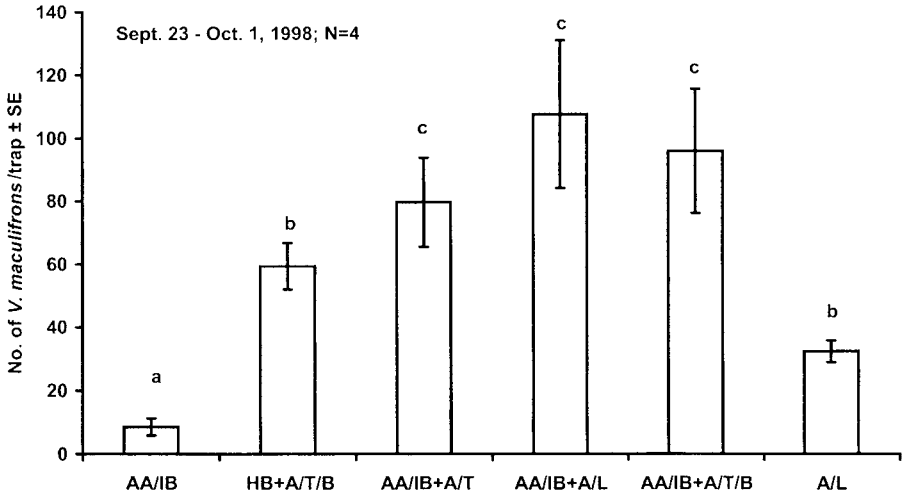

Fig. 3. Mean number of *Vespula maculifrons* workers (±SE; n = 4) caught from September 23 through October 1, 1998, in traps baited with acetic acid/isobutanol (AA/IB) and/or (*E*)-2-hexenal/monoterpenol-based lures (L = linalool; other abbreviations as in Fig. 2). Means followed by the same letter are not significantly different ($P > 0.05$).

Here we demonstrated a secondary level of synergism in which two volatile blends, (*E*)-2-hexenal plus linalool or α-terpineol and acetic acid plus isobutanol, together act synergistically to attract yellowjackets in the *V. vulgaris* species group. Based on previous yellowjacket trapping in Maryland (Aldrich et al. 1985, Aldrich et al. 1986), among the *V. rufa* group of species (Akre et al. 1981) *V. vidua* would be expected to be present in collections, yet no individuals of this species were caught. The Southern yellowjacket, *V. squamosa,* listed by Akre et al. (1981) as a species of "uncertain status", was caught in significant numbers at two sites (the private residence and the apiary). At the private residence site the synergism was indicated (Table 1), whereas at the apiary site there was no difference in attraction of *V. squamosa* to (*E*)-2-hexenal with linalool or α-terpineol plus the acetic acid/isobutanol mixture compared to the acetic acid/isobutanol mixture alone.

The discovery of a second order synergism for yellowjacket attraction may be useful from a practical standpoint in formulating better wasp lures, particularly for eastern U.S. species of yellowjackets that are only weakly attracted to heptyl butyrate. (*E*)-2-Hexenal diethyl acetal is deemed a more desirable compound for this type of lure than (*E*)-2-hexenal itself because this commercially available acetal is less volatile and more stable than (*E*)-2-hexenal and, under acetic conditions, gradually degrades to (*E*)-2-hexenal and ethanol. Solid-phase microextraction analyses of a lure made with (*E*)-2-hexenal diethyl acetal showed that this acetal is totally degraded in acidified water to release (*E*)-2-hexenal, which readily evaporates from the water (Fig. 1). Although ethanol was detected among the volatiles from the lure without any water added (Fig. 1A), no ethanol was detected in the headspace over acidified water (Fig. 1B), presumably because the ethanol largely remains in aqueous solution. The failure

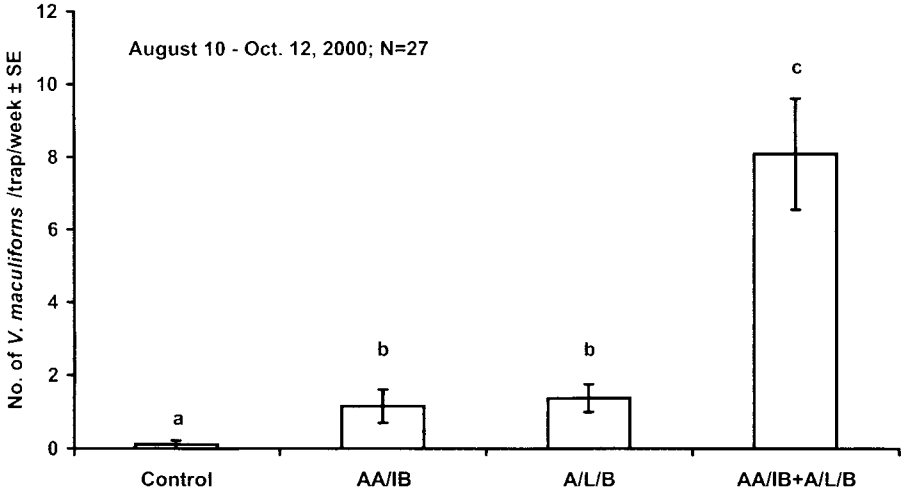

Fig. 4. Mean number of *Vespula maculifrons* workers (±SE; n = 27) caught per week from August 10 through October 12, 2000, in traps baited with acetic acid/isobutanol (AA/IB), (*E*)-2-hexenal diethyl acetal/linalool/benzyl alcohol (A/L/B), AA/IB + A/L/B, and unbaited control traps. Means followed by the same letter are not significantly different ($P > 0.05$).

Table 1. Captures of yellowjackets and paper wasps in traps deployed at a private residence in Silver Spring, Maryland, from September 8-18, 2000

Species	Treatments*			
	Control	A/L/B	AA/IB	AA/IB + A/LB
Vespula squamosa	5^{a}	4^{a}	8^{a}	34^{b}
V. vidua	0	2	0	0
V. maculifrons	0^{a}	4^{b}	6^{b}	44^{c}
V. germanica	6^{a}	25^{b}	8^{a}	165^{c}
V. flavopilosa	0	0	2^{a}	23^{c}
Polistes dominulus	1^{a}	2^{a}	4^{ab}	11^{b}
Other *Polistes* spp.	1	2	2	1

* Captures within a row (=species) followed by the same superscript letter are not significantly different based on the Chi-square goodness of fit test at $\alpha = 0.05$ level.

to detect ethanol in the acidified water containing the lure (Fig. 1C) may be due to differential adsorption in water versus air on the non-polar SPME fiber (Bartelt 1997); in fact, the non-polar fiber used in our analyses failed to detect acidic acid in either water or headspace. In any case, ethanol does not appear to be involved in the

synergism documented here, and may simply help kill yellowjackets caught in the water inside the traps. Linalool is the preferred monoterpenol for this lure so as to avoid killing the spined soldier bug, *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae), a common predator of caterpillars and beetle larvae in North America (Aldrich et al. 1984), which is attracted to the combination of (*E*)-2-hexenal and α-terpineol. Benzyl alcohol, a component of the *P. maculiventris* pheromone, did not influence attraction of yellowjackets at the level tested.

From a theoretical standpoint, it is interesting to consider why a synergism between the acetic acid/isobutanol blend and the hexenal/monoterpenol blends occurs. Wasp attraction to heptyl butyrate and to acetic acid with isobutanol is thought to be a strategy to locate sugars (Reed and Landolt 2002). The Western yellowjacket, *V. pensylvanica,* is unique among yellowjackets in that workers are attracted to both heptyl butyrate and acetic acid with isobutanol (Reed and Landolt 2002), two odors apparently associated with different carbohydrate sources. Nevertheless, the combination of heptyl butyrate and acetic acid/isobutanol resulted in an additive increase in attraction rather than a synergism (Landolt 1998). In contrast to these sugar-associated odors, hexenal/monoterpenol blends appear to constitute damaged leaf odors associated by yellowjackets with the presence of phytophagous prey (Aldrich et al. 1985). The latter interpretation is substantiated by research on two different paper wasp species (Cornelius 1993, Richter 2000) showing that foragers preferentially respond to leaves with caterpillar feeding damage (see also, Spurr 1995). Our results indicate that combining volatile chemicals associated with carbohydrate feeding (acetic acid/isobutanol) and volatiles associated with foraging for insect prey (hexenal/α-terpineol or linalool) results in a truly synergistic response by workers of *V. maculifrons* and other members of the *V. vulgaris* species group.

Among various insect groups for which attractant pheromones have been identified it is increasingly evident that host-associated kairomones synergize responses to pheromones. Green leaf volatiles (GLVs), for example, have been shown to synergize pheromonal attraction of the boll weevil, *Anthonomus grandis* Boheman; the smaller European elm bark beetle, *Scolytus multistriatus* (Marsham); the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Dickens et al. 1990); and various moth species (Dickens et al. 1993, Light et al. 1993). Different GLV compounds often function additively or may be redundant yet, when combined with a pheromone, yield a synergistic response (Aldrich et al. 2003). Similarly, induced plant volatiles such as methyl salicylate (Aldrich et al. 2003) can synergize pheromone attraction; for example, methyl salicylate itself was unattractive to the goldeneyed lacewing, *Chrysopa oculata* Say (Neuroptera: Chrysopidae), but this plant volatile synergized attraction of *C. oculata* males to the pheromone compound, iridodial (Zhang and Aldrich 2004). It is now known that GLVs act synergistically with certain volatiles characteristic of deciduous tree bark to inhibit attraction of conifer-specific bark beetles, again with redundancy among the compounds within each kairomone type (i.e., leaf or bark volatiles) (e.g., Zhang and Schlyter 2003). Thus, additive or redundant effects within a semiochemical type seem common; whereas, combinations of different types of semiochemicals often result in synergistic responses. Indeed, presenting visual signals simultaneously with olfactory signals to *V. germanica* workers leads to synergistic attraction (D'Adamo et al. 2003).

For wasps, it has been suggested that foraging for protein resources may somehow differ fundamentally from foraging for carbohydrate resources (Richter and Tisch 1999). Our results tend to corroborate the idea that in yellowjackets there is some

neurophysiological difference between carbohydrate and protein foraging such that combining the kairomonal signals associated with each type of foraging elicits a synergistic response.

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