Journal of Chemical Ecology, Vol. 25, No. 5, 1999

OLFACTORY REACTIONS OF THE TWELVE-SPOTTED LADY BEETLE, *Coleomegilla maculata* AND THE GREEN LACEWING, *Chrysoperla carnea* TO SEMIOCHEMICALS RELEASED FROM THEIR PREY AND HOST PLANT: ELECTROANTENNOGRAM AND BEHAVIORAL RESPONSES

JUNWEI ZHU,[1,*] ALLARD A. COSSÉ,[1,3] JOHN J. OBRYCKI,[1]
KYUNG SAENG BOO,[2] and THOMAS C. BAKER[1]

[1]*Department of Entomology*
Iowa State University
Ames, Iowa 50011

[2]*Department of Agricultural Biology*
Seoul National University
Suwon 441-744, Korea

[3]*NCAUR/ARS/USDA*
1815 N University St., Peoria, Illinois 61604

(Received June 15, 1998; accepted January 12, 1999)

Abstract—Electroantennograms (EAGs) were recorded from two predatory insect species, the twelve-spotted lady beetle, *Coleomegilla maculata* and the green lacewing, *Chrysoperla carnea* in response to semiochemicals emitted from one of their prey species, the pea aphid *Acyrthosiphon pisum* and their host plant. EAG responses were also recorded from *C. maculata* in response to extracts from individuals of the opposite sex and to extracts from an herbaceous plant, catnip *Nepeta cataria*. Extracts of catnip and two sex pheromone components of aphids, (4a*S*,7*S*,7a*R*)-nepetalactone and (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol, elicited significant EAG responses from the antennae of both predatory species. Of 10 corn volatile compounds tested, *C. carnea* adults responded most strongly to 2-phenylethanol and (*E*)-β-farnesene. A significant difference in EAG response to extracts of corn leaf collections was observed between male and female *C. carnea*. In *C. maculata*, significant EAG responses were elicited by most of the tested corn volatile compounds, except α-pinene and (*E*)-2-hexenal. The highest EAG responses were observed in response to (*E*)-β-farnesene,

*To whom correspondence should be addressed.

0098-0331/99/0500-1163$16.00/0

α-terpineol, 2-phenylethanol, and β-caryophyllene. Sexual differences in EAG responses of *C. maculata* were only found in response to 1-octen-3-ol. Male antennae of *C. maculata* produced significant EAG responses to extracts from conspecific females, but not to males, which indicates that some chemicals from females could be involved in sexual communication. A significant EAG response also was recorded in response to the extracts of fluids produced during "reflex bleeding." Male and female antennae of both species exhibited similar dose–response curves to most of the selected compounds, although female *C. maculata* antennae exhibited higher thresholds in response to several compounds including α-terpineol, (Z)-3-hexenol, and (4a*S*,7*S*,7a*R*)-nepetalactone. Field tests showed that 2-phenylethanol was highly attractive to both sexes of the two investigated species. Only *C. maculata* was attracted to traps baited with α-terpineol.

Key Words—Electroantennograms, dose–response, trapping test, corn volatile compound, aphid sex pheromone, catnip, aphid alarm pheromone, *Coleomegilla maculata*, Coccinellidae, *Chrysoperla carnea*, Chrysopidae.

INTRODUCTION

The use of predatory insects, including coccinellids and chrysopids, as biological control agents to suppress pest populations on either economically important crops or in home gardens is widely accepted and recognized by the general public and biological control practitioners (see references in Obrycki and Kring, 1998; Canard et al., 1984). There have been significant successes in using coccinellids and chrysopids to suppress whitefly, aphid, mealybug, scale, and mite populations (Gerling, 1990; Frazier, 1988; New, 1975). Despite the significant use of these two groups of predatory insects for biological control, very little is known about the mechanisms involved in prey location (van Emden and Hagen, 1976; Hagen, 1987). In particular, it is not known whether the predators are able to use odors directly from their prey or their host plant to eventually locate their prey. Because of the dispersal behavior of many aphidophagous species and their polyphagous nature (Frazier, 1988), attractive compounds could be useful in retaining predaceous insects in fields where they were released.

The twelve-spotted lady beetle, *Coleomegilla maculata* (Degeer) (Coleoptera: Coccinellidae), and the golden eyed green lacewing, *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae), are two of the most common aphid predators found in field crops in the eastern United States. They are especially abundant in crops such as cotton, corn, and alfalfa. In corn these two predatory species feed on aphids and European corn borers (Obrycki and Kring, 1998; Phoofolo, 1997; Sparks et al., 1966; Udayagiri, 1996), and in alfalfa they feed on aphids and alfalfa weevil larvae (Giles et al., 1994). In the present study we report results of electroantennogram (EAG) and behavioral responses of *C. carnea* and *C. maculata* to selected semiochemicals released from corn leaves and from an aphid prey, the pea aphid *Acyrthosiphon pisum.* (Homoptera: Aphididae). The possible existence of sex pheromone compounds in *C. maculata* was also investigated.

METHODS AND MATERIALS

Insects. Coleomegilla maculata adults were collected from an overwintering site in Roland, Iowa. Larvae of *C. carnea* were purchased from Rincon-Vitova, California, and reared at 20°C and 16L : 8D period. Females were mated and produced eggs. Larvae were fed with pea aphids *A. pisum* and frozen *Ephestia kuehniella* eggs until pupation. Adults were sexed and kept in separate cages until used in experiments.

Extraction of Potential Sex Pheromone-like Substances from C. maculata. Adults of both sexes were anesthetized by placing them at −20°C, and the abdomen and elytra of adults were cut off with a pair of fine scissors. Dissecting tools were rinsed with acetone several times between dissections to avoid cross-contamination. The dissected parts were extracted in a 1-ml vial containing 500 μl of hexane for 2 hr. Ten males and 10 females were dissected and extracted. The extracts were concentrated to 200 μl under a mild stream of N_2. Approximately 20 μl of the extracts, equivalent to one adult, were used for the EAG tests.

Collection of Defensive Compound Extracts. Both sexes of *C. maculata* were handled vigorously and pressed against a piece of filter paper (Whatman, No. 1), resulting in reflex bleeding production of orange-colored fluid excreted through the joints of the legs. The fluid was absorbed into filter paper; fluid from 20 beetles was collected. The filter paper used for the collection was then cut into small pieces and placed in a 2-ml vial and extracted with 200 μl of hexane for 1 hr. A volume of 10 μl of the concentrated extract was used for EAG tests.

Collection of Plant Volatiles. Corn (Pioneer, Hybrid 3489) was grown in the greenhouse under approx. 25°C and 75% humidity, with natural light supplemented by 400-W high-pressure sodium lights. The three-leaf stage of plants was used for volatile collections because this life stage is infested by corn leaf aphids (Bing et al., 1992), and it is also a stage searched by these predatory species. Corn leaves were removed from plants, and ca. 15 g placed in a 0.5-liter glass collector with two openings on each side. A stream of purified air passing through a freshly activated charcoal filter was blown into the inlet of the collector, through the corn leaves, and exited through the outlet connected to a Tenax trap. The trap consisted of a Pasteur pipet (5 cm long and 0.5 cm diameter) packed with 300 mg of Tenax (20–35 mesh, Alltech, Illinois). The flow rate of the air was 150 ml/min from the outlet of the Tenax trap, and the volatiles were collected for 18 hr. The trapped volatiles were eluted with HPLC-grade hexane.

The extracts from three collections were combined and concentrated to 100 μl. Ten microliters of extracts were used for each EAG test.

Extracts of Catnip. Dried seeds and flowers of catnip *Nepeta cataria* were purchased from a local pet store. For EAG tests, approx. 0.2 mg of dried plant material was homogenized and extracted by adding 500 μl of hexane. The extract was poured through a funnel with filter paper (Whatman No. 1), and the residue was discarded. The extract was concentrated to 100 μl under a mild stream of N_2. The extract was stored at $-20°C$ until used in EAG tests.

Electroantennogram Responses. EAG recordings were made by connecting an electrogel-filled (Spectro 360, Parker Laboratory, New Jersey) glass pipet Ag–AgCl electrode to the excised head from a beetle or a lacewing. A recording electrode filled with the same electrogel connected to a high-impedance DC amplifier with automatic baseline drift compensation was placed in contact with the tip of the antennae. Antennal responses to various chemical stimuli were first recorded for a series of commercial synthetic compounds representing known corn leaf volatiles. Then, male and female body extracts of *C. maculata*, reflex bleeding extracts, aphid alarm pheromone, and catnip extracts were tested. A second series of EAG tests was then conducted including a dose–response series with selected EAG-active compounds from the first test. Serial dilutions of the tested compounds were made in redistilled HPLC-grade hexane at dosages ranging from 0.1 to 1000 μg, except 2-phenylethanol, for which methylene chloride was used as the solvent. The tested compounds and extracts were applied to filter-paper strips (0.5×2.5 cm, Whatman No. 1) in 10 μl of solvent, except as otherwise noted. The filter-paper strips were inserted into Pasteur pipets (15 cm long). Control puffs of air were applied after each puff of a test stimulus. The response to the air puff was used to normalize beetle or lacewing responses relative to the tested stimuli. The average EAG response to the air puff from antennae of *C. maculata* and *C. carnea* was 0.05 ± 0.003 mV ($N = 30$) and 0.02 ± 0.001 mV ($N = 27$), respectively. The relative EAG response of each stimulus was normalized by dividing the amplitude of the test stimulus by the mean of the response to the control puff. The sequence of exposure of each stimulus to each antenna was randomly defined.

Chemicals. Ten corn volatile compounds were used, and the source and purity of these compounds are listed in Table 1. The two aphid sex pheromone components, (4a*S*,7*S*,7a*R*)-nepetalactone and (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol were kindly provided by Dr. John Pickett of the IACR-Rothamsted, UK. The purity of these two compounds was approx. 97% and 55%, respectively, as analyzed by GC-MS.

Field Test. A preliminary field trapping test was conducted in an alfalfa field in Ames, Iowa. Synthetic compounds were prepared in hexane or methylene chloride. Medical peerless cotton rolls (5 cm long, 100% cotton) impregnated with a dose of 50 mg of each compound were used as dispensers, and the traps

TABLE 1. SOURCE AND PURITY OF CORN VOLATILE COMPOUNDS USED IN EAG TESTS

Compound	Source of supply	Purity (%)[a]
(*E*)-β-Farnesene	Bedoukian Research Inc.	>99
α-Terpineol	Bedoukian Research Inc.	>99
α-Pinene	Aldrich Chemical Co.	95
(*Z*)-3-Hexenal	Bedoukian Research Inc.	>99
2-Phenylethanol	Bedoukian Research Inc.	>99
(*E*)-2-Hexenal	Sigma Chemical Co.	>99
β-Caryophyllene	K & K Laboratories	>98
1-Hexanol	Sigma Chemical Co.	98
(*Z*)-3-Hexenol	Bedoukian Reserach Inc.	>99
1-Octen-3-ol	Bedoukian Research Inc.	>99

[a]Label information

used were similar to the Rebell Trap (Great Lakes IPM, Michigan). The trap was hung from the bent end of an electric farm post, 1.2 m above the ground. Within a replicate ($N = 3$), traps were set at least 10 m apart. The traps were checked daily, and trap position within a series was randomized to minimize the effects of habitat heterogeneity.

Statistics. The resulting EAG data (means of relative responses) and trap catches (means of trapped species) were compared by analysis of variance followed by Fisher's protected least significant difference test (FPLSD).

RESULTS

Selectivity. In general, the antennae of both sexes of the two predatory species, *C. maculata* and *C. carnea*, responded strongly to several green leaf volatiles and sex pheromones of their aphid prey. No obvious differences in the sizes and morphologies of their receptor organs were observed between the two sexes of the same species. Within each species, slight differences in EAGs to each of the tested stimuli were noted, but only two of them were statistically different.

Response to Crude Extracts. In *C. maculata*, female extracts of both the whole abdomen and the elytra elicited higher EAG responses from male antennae compared with those of male extracts (Figure 1). The extracts from the defensive reflex bleeding also elicited EAG responses. Both male and female antennae responded strongly to catnip extracts (Figure 2). In *C. carnea*, no significant EAG responses were observed when stimulated with the extract of *C. maculata* reflex bleeding (data not shown here), but significant EAG responses were elicited when tested with catnip extracts (Figure 3). EAG response of female *C. carnea* antenna to extracts of corn leaves was greater than that of the males.

Response to Corn Leaf Volatiles. Ten common corn leaf volatiles, previously

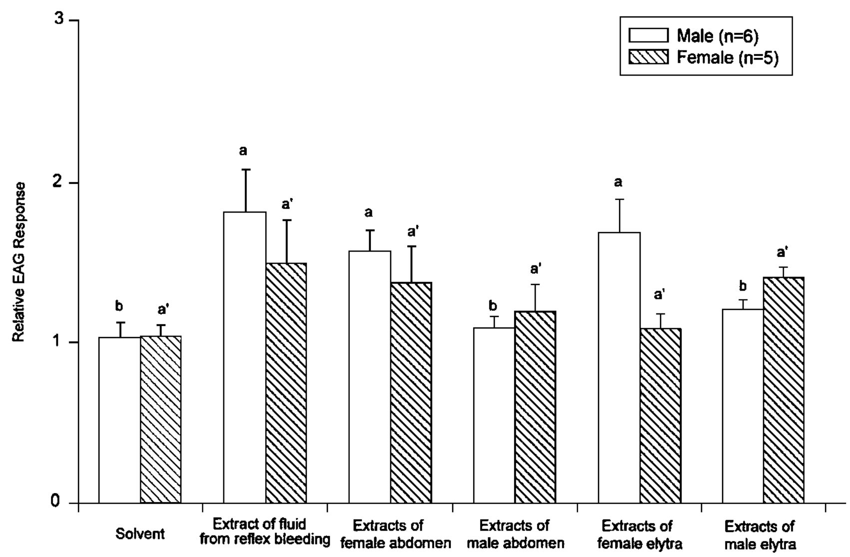

FIG. 1. EAG responses of male and female *Coleomegilla maculata* to various extracts from conspecific body parts and the fluid of reflex bleeding. Means (± standard error) with no letters in common are significantly different (ANOVA followed by FPLSD test, $P < 0.01$).

identified from corn leaves (Buttery and Ling, 1984), were selected for a standard EAG test. In both sexes of *C. maculata*, antennae responded to most of the tested compounds. Responses to (*E*)-β-farnesene, α-terpineol, and 2-phenylethanol were significantly higher than those to α-pinene of (*E*)-2-hexenal (Figure 2). However, a significantly higher EAG response was elicited by 1-octen-3-ol from male antenna, relative to that from a female (Figure 2). In *C. carnea*, only two corn volatile compounds elicited significant EAG responses, with a significant response from 2-phenylethanol and (*E*)-β-farnesene, respectively (Figure 3).

Response to Sex Pheromone and Alarm Pheromone of Aphids. Both sexes of the two investigated species responded to sex pheromone components used by their prey species, (4a*S*,7*S*,7a*R*)-nepetalactone and (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol. In *C. maculata*, a relatively higher EAG response was elicited by (4a*S*,7*S*,7a*R*)-nepetalactone than that by the alcohol (Figure 2). Aphid alarm pheromone, (*E*)-β-farnesene, elicited EAG responses from male antennae as high as those in response to aphid sex pheromone. In *C. carnea*, there were no significant differences between male and female EAGs to aphid sex pheromone components (Figure 3). However, female antennae of *C. carnea* responded to (4a*S*,7*S*,7a*R*)-nepetalactone greater than to (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol.

Sensitivity. EAG responses in *C. maculata* generally increased with increas-

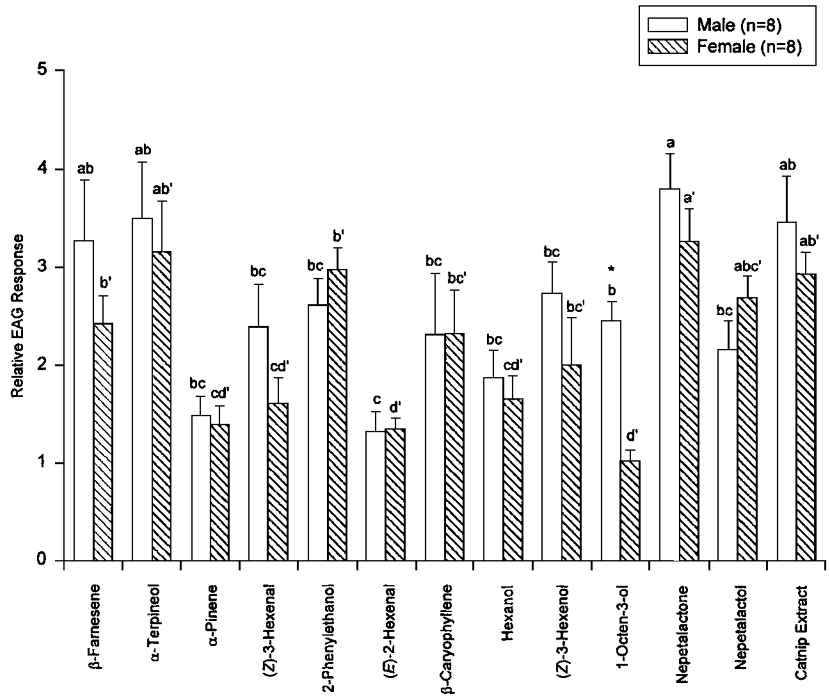

FIG. 2. EAG responses of male and female antennae of *Coleomegilla maculata* to several synthetic corn leaf volatile compounds, sex pheromone components of aphids and the crude extract of catnip. Means (± standard error) with no letters in common are significantly different (ANOVA followed by FPLSD test, $P < 0.05$). An asterisk above the letter indicates a significant difference in EAGs between male and female antennae in response to this compound (Student's t test, $P < 0.001$).

ing doses of the selected synthetic corn volatile compounds (Figure 4). EAG dose–response curves showed that male antennae reached saturation at the dose of 100 μg for two of the tested corn volatile compounds, (*E*)-β-farnesene and α-terpineol (Figure 4). Female antennae appeared to be relatively sensitive to α-terpineol and 2-phenylethanol, with significant EAG responses elicited at a dose of 10 μg. In response to (4a*S*,7*S*,7a*R*)-nepetalactone and (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol, the minimum dose for a significant EAG response from both male and female antennae was 100 μg, and saturation likewise occurred at this same dose (Figure 4).

In *C. carnea*, response curves of both male and female antennae in response to the tested corn volatile compounds exhibited significant differences in response sensitivity (Figure 5). EAG responses of both sexes to (*E*)-β-farnesene increased

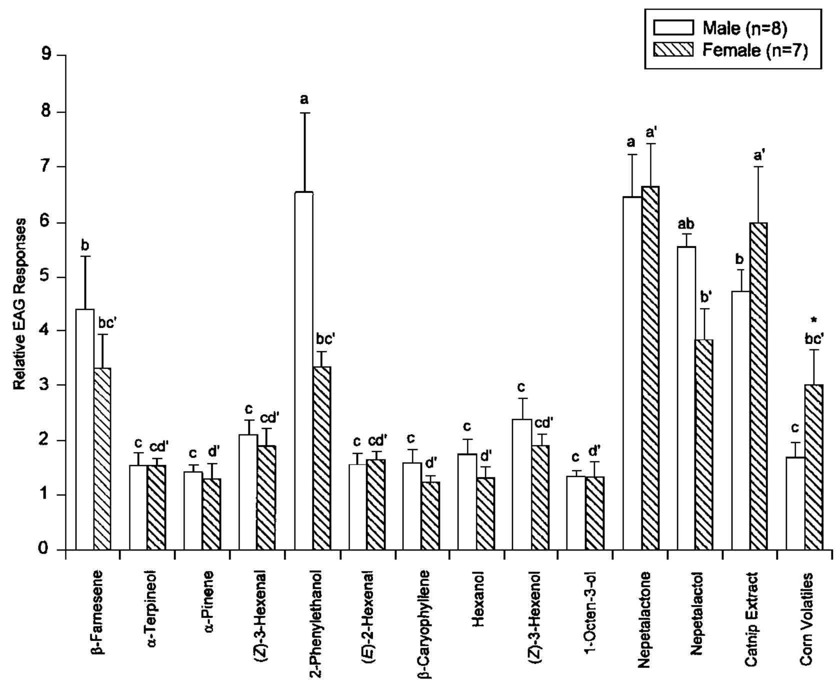

FIG. 3. EAG responses of male and female antennae of *Chrysoperla carnea* to several synthetic corn leaf volatile compounds, sex pheromone components of aphids and the crude extract of catnip. Means (± standard error) with no letters in common are significantly different (ANOVA followed by FPLSD test, $P < 0.05$). An asterisk above the letter indicates a significant difference in EAGs between male and female antennae in response to this compound (Student's t test, $P < 0.05$).

with increasing doses, and the highest EAG response was observed at a dose of 1000 μg. Significant EAG responses were elicited from the antennae of both sexes to 2-phenylethanol at 100 μg dosage. No significant differences in EAG responses among the three higher tested doses of this compound were observed. In contrast, α-terpineol and (Z)-3-hexenol from corn elicited relatively lower EAG responses at all dosages tested. For the two aphid sex pheromone components, the same trends were observed as those shown in *C. maculata*. Saturation appeared at a dose of 100 μg for both compounds in both sexes.

Field Tests. The results from our preliminary field trapping test showed that both species were attracted to one of tested corn volatile compounds, 2-phenylethanol (Figure 6). In addition, still higher catches of *C. maculata* were observed in traps baited with α-terpineol.

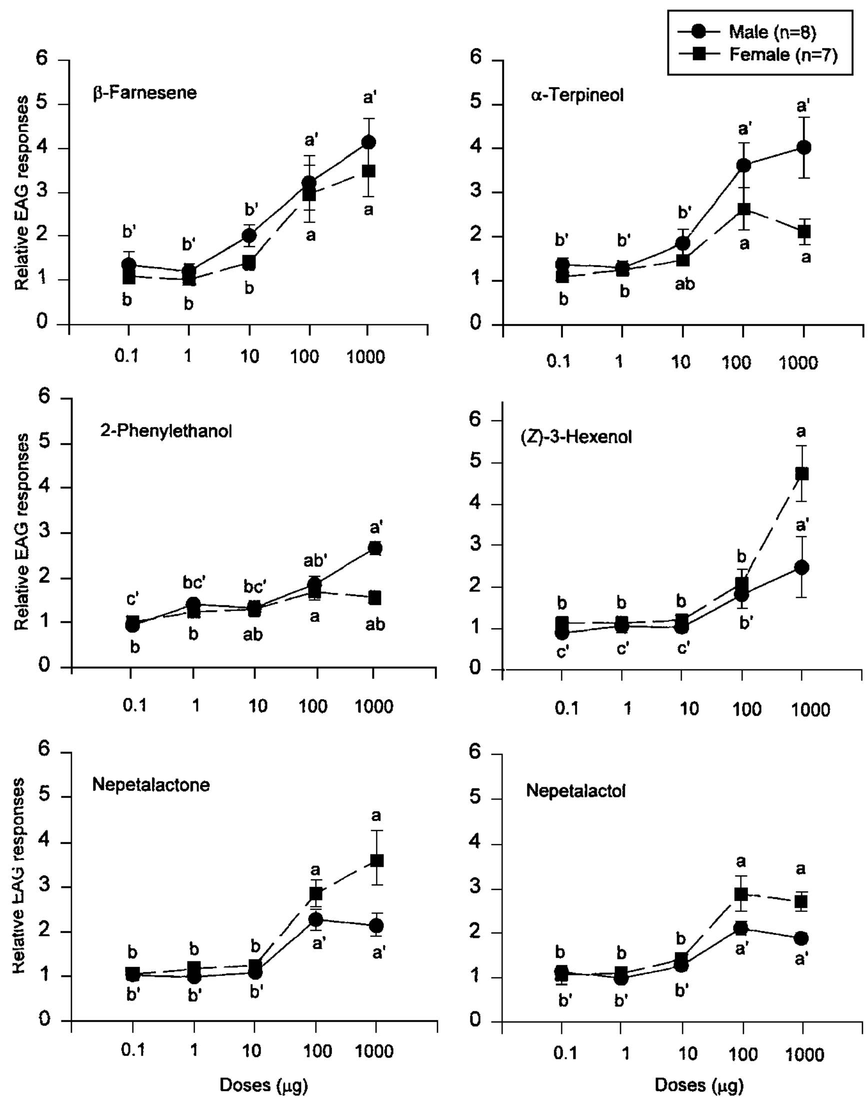

FIG. 4. Dose–response curves constructed from EAGs of male and female of *Coleomegilla maculata* to four synthetic corn leaf volatile compounds and two sex pheromone components of aphids. Means (± standard error) of different dosages among the same stimulus with no letters in common are significantly different (ANOVA followed by FPLSD test, $P < 0.05$).

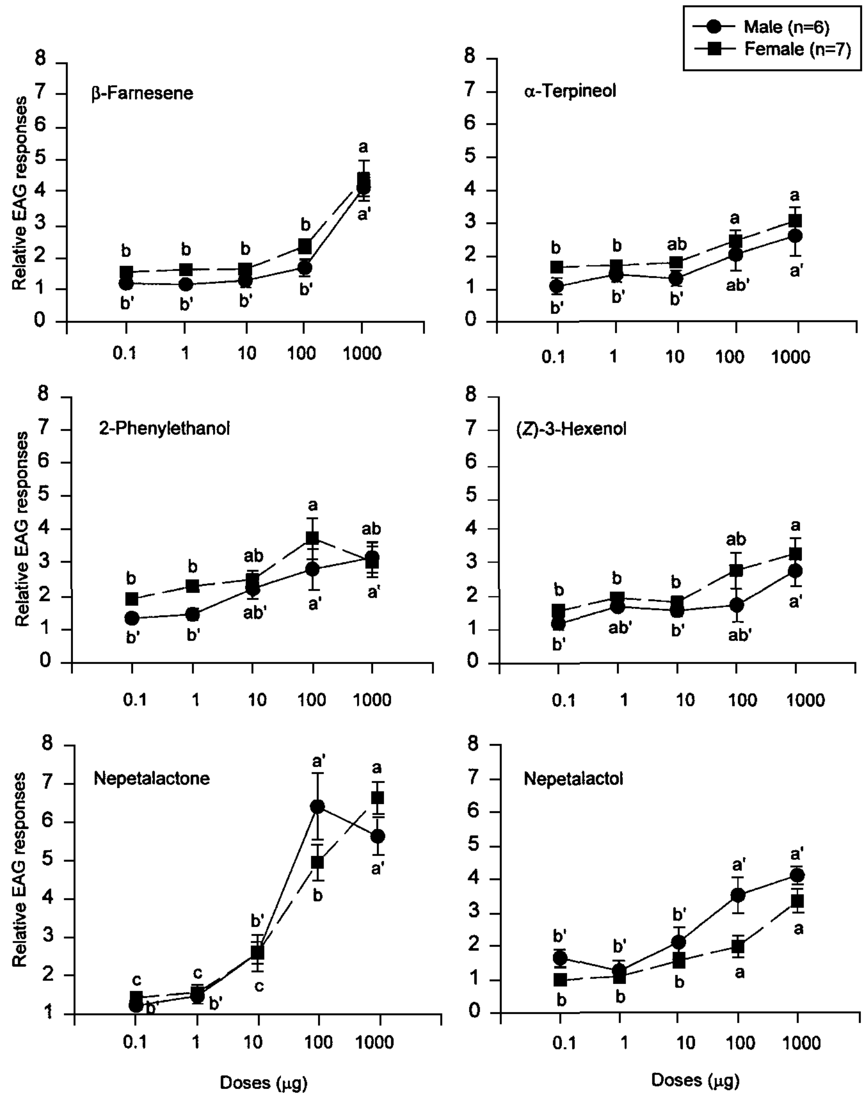

FIG. 5. Dose–response curves constructed from EAGs of male and female of *Chrysoperla carnea* to four synthetic corn leaf volatile compounds and two sex pheromone components of aphids. Means (± standard error) of different dosages among the same stimulus with no letters in common are significantly different (ANOVA followed by FPLSD test, $P < 0.05$).

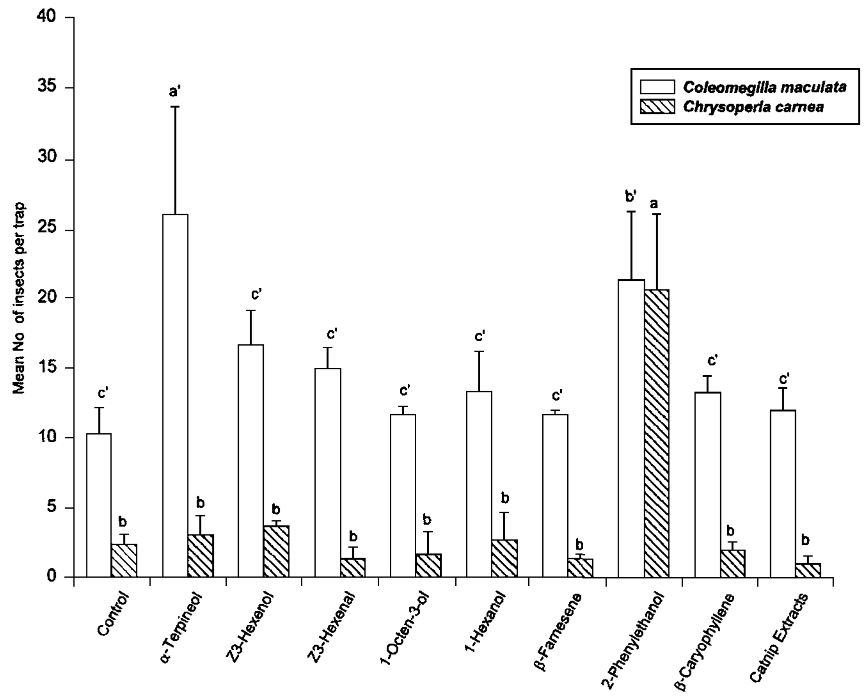

FIG. 6. Mean number of *Coleomegilla maculata* and *Chrysoperla carnea* caught in traps baited with corn volatile compounds (50 mg) and crude extracts of catnip in the alfalfa field (line indicates SE) (± standard error). For each species, columns with no letters in common are significantly different (ANOVA followed by FPLSD test, $P < 0.05$).

DISCUSSION

To our knowledge, this is the first published report of successful EAG recordings from the two predatory insect species, *C. maculata* and *C. carnea*. The significant EAG responses to semiochemicals released from their potential prey species and their host plants indicate that these two predators could possibly use such chemicals to locate their prey. These EAG-active compounds, if they prove to have behavioral activities as attractants or arrestants, could possibly be used to enhance the efficacy of these two predaceous insects in pest management systems. Emitting these compounds in cropping systems could attract lady beetles and lacewings to their target habitats and retain them in habitats for longer durations.

Volatiles from corn plants contain general and specific odor components including green leaf alcohols, aldehydes, derivative esters, terpenes, and sesquiterpenes (Buttery and Ling, 1984). Many parasitoids use semiochemicals associated with the host or the host habitat to locate their prey (Udayagiri, 1996; Turlings et al., 1992). In coccinellids, only Obata (1987) has reported that chemical cues could be involved in prey finding. EAG responses from the antennae of *C. maculata* elicited by corn volatile components including (*E*)-β-farnesene, α-terpineol, 2-phenylethanol, β-caryophyllene, (*Z*)-3-hexenol, hexanol, and 1-octen-3-ol demonstrate that this predator could possibly respond to odors from host habitats for prey location. Our preliminary field trapping results showed that adult *C. maculata* were attracted to at least two components, α-terpineol and 2-phenylethanol. Approximately equal numbers of both sexes were caught in traps.

Among the seven corn volatile compounds found to be EAG-active in *C. maculata*, (*E*)-β-farnesene has also been reported as an aphid alarm pheromone component (Nault et al., 1973). This compound is emitted from aphids when they are disturbed. The perception of this pheromone by aphids leads to dispersal from their feeding sites. Results of our preliminary behavioral tests show that two lady beetle species, *Hippodamia convergens* and *Harmonia axyridis*, are attracted by this compound (data not shown here). This compound, however, does not elicit searching behaviors in another lady beetle, *Coccinella septempunctata* (Nakamuta, 1991). The active EAG response recorded from the antennae of *C. maculata* to this compound could also be a result of responding to corn volatiles, because (*E*)-β-farnesene is also a common compound among corn leaf volatiles, although it is generally found together with other sesquiterpene hydrocarbons. Colburn and Asquith (1970) have showed that odors from mites feeding on plants, including (*E*)-β-farnesene, are used by adults of the ladybird beetle *Stethorus punctum* to select host plants. However, no differences in catches were found from the traps baited with this compound compared to those of the control.

Chemicals secreted by aphids other than (*E*)-β-farnesene, such as breakdown products of honeydew, are known to cue local search by lady beetles (Evans and Richards, 1997). Sex pheromone communication in mate finding was demonstrated in aphids in the genus *Schizaphis* (Pettersson, 1970). Virgin females (oviparae) release a male-attracting pheromone from scent plaques on their metathoracic tibiae. Dawson et al. (1989) identified sex pheromones of several aphid species as a combination of (4a*S*,7*S*,7a*R*)-nepetalactone and (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol. It has been suggested that female parasitoids may use this aphid sex pheromone as a kairomone to locate females of their holocyclic aphid hosts (Hardie et al., 1994). The present study shows that antennae of adult *C. maculata* responded with significant EAGs to these two components of aphid sex pheromone, which indicates that *C. maculata* may use them or similar compounds in prey finding. Significant EAG responses were also observed from the antennae of *C. maculata* in response to the extract of catnip, which may be explained because (4a*S*,7*S*,7a*R*)-nepetalactone is a major constituent in essential oil of *N. cataria* (Eisenbraun et al., 1980).

Because adult *C. carnea* are reported most active at twilight or during the night (Duelli, 1984) when the use of visual cues might be impaired, significant EAG responses to plant volatile compounds and sex pheromones of their prey species suggest that chemical orientation may be involved in prey host location. Van Emden and Hagen (1976) found that tethered *C. carnea* females responded positively in flight toward isomers of tryptophan and their breakdown products. Our results show that the antennae of *C. carnea* are highly sensitive to two corn leaf volatiles, (E)-β-farnesene and 2-phenylethanol. However, in the field trapping test *C. carnea* adults were only attracted to the latter compound. Both sexes of lacewings were caught in the traps baited with 2-phenylethanol. Female catches were significantly higher than males (data not shown here). The recorded EAG response to (E)-β-farnesene from *C. carnea* is different from the results obtained from the Asian lacewing *Chrysopa cognata* (Boo et al., 1998). Significant EAG responses elicited by 2-phenylethanol at a relatively lower dose may indicate the ability of *C. carnea* to detect the compound at a greater distance from its source. Further behavioral studies to test this hypothesis are being conducted.

An earlier study showed that β-caryophyllene acts as an attractant to adults of *C. carnea* in the field (Flint et al., 1979). However, our present EAG study showed a relatively low EAG response obtained from the antennae of *C. carnea* and low catches of *C. carnea* in a field test. The significant EAG responses from *C. carnea* to sex pheromones of their prey aphid species presented here suggest that both males and females could possibly locate their prey by responding to these compounds. Recently Boo et al. (1998) reported that adult *C. cognata* are attracted to (4a*S*,7*S*,7a*R*)-nepetalactone and mixtures of this compound with (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol in the field.

The search for sex pheromones in Coccinellidae during the last decade has not been successful. However, recent studies on the ultrastructure of integumentary glands in the coccinellid *Semiadalia undecimnotata* as well as specific olfactory sensilla types clustered on the two distal segments of the antennae may indicate the possible involvement of long-range chemosensory perception (Barbier et al., 1992; Jourdan et al., 1995). In our present EAG experiments, we demonstrated that the female extracts of *C. maculata* elicited significant EAG responses from male conspecific antennae, which suggest that the substances from females could be used as sex pheromone for mate finding.

Acknowledgments—The authors would like to express their thanks to Bess Lewis, Anna Keyte, and Brad Tucker for rearing the predatory insects, and Jennifer Harris for assisting the field tests. This project was supported by a grant (98-72) from the Leopold Center for Sustainable Agriculture. Journal Paper No. J-18333 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa, Project No. 3240, and supported by Hatch Act and State of Iowa funds.

REFERENCES

BARBIER, R., FERRAN, A., LE LANNIC, J., and ALLO, M.-R. 1992. Morphology and ultrastructure of integumentary glands of *Semiadalia undecimnotata* Schn. (Coleoptera: Coccinellidae). *Int. J. Insect Morphol. Embryol.* 21:223–234.

BING, J. W., GUTHRIE, W. D., DICKE, F. F., and OBRYCKI, J. J. 1992. Seedling stage feeding by corn leaf aphid (Homoptera: Aphididae): Influence on plant development in maize. *J. Econ. Entomol.* 84:625–632.

BOO, K. S., CHUNG, I. B., HAN, K. S., PICKETT, J. A., and WADHAMS, L. J. 1998. Response of the lacewing *Chrysopa cognata* Wesmael (Neuroptera: Chrysopidae) to pheromones of its aphid (Homoptera: Aphididae) prey. *J. Chem. Ecol.* 24:631–643.

BUTTERY, R. G., and LING, L. C. 1984. Corn leaf volatiles: Identification using Tenax trapping for possible insect attractants. *J. Agric. Food Chem.* 32:1104–1106.

CANARD, M., SÉMÉRIA, Y., and NEW, T. R. 1984. Biology of Chrysopidae. Dr. W. Junk, The Hague, 294 pp.

COLBURN, R., and ASQUITH, D. 1970. A cage used to study the finding of a host by the ladybird beetle, *Stethorus punctum*. *J. Econ. Entomol.* 63:1376–1377.

DAWSON, G. W., JANES, N. F., MUDD, A., PICKETT, J. A., SLAWIN, A. M. Z., WADHAMS, L. J., and WILLIAMS, D. J. 1989. The aphid sex pheromone. *Pure Appl. Chem.* 61:555–558.

DUELLI, P. 1984. Flight, dispersal, migration, pp. 129–133, *in* M. Canard, Y. Semeria and T. R. New (eds.). Biology of Chrysopidae. W. Junk, The Hagu.

EISENBRAUN, E. J., BROWNE, C. E., IRVIN-WILLIS, R. L., MCGRUK, D. J., ELIEL, E. L., and HARRIS, D. L. 1980. Structure and stereochemistry of $4a\beta,7\alpha,7a\beta$-nepetalactone from *Nepta mussini* and its relationship to the $4a\alpha,7\alpha,7a\alpha$- and $4a\alpha,7\alpha,7a\beta$-nepetalactone from *N. cataria*. *J. Org. Chem.* 45:3811–3814.

EVANS, E. W., and RICHARDS, D. R. 1997. Managing the dispersal of ladybrid beetles (Col: Coccinellidae): Use of artificial honeydew to manipulate spatial distributions. *Entomophaga* 42:93–102.

FLINT, H. M., SLATER, S. S., and WALTERS, S. 1979. Caryophyllene: An attractant for the green lacewing. *Environ. Entomol.* 8:1123–1125.

FRAZIER, B. D. 1988. Coccinellidae, pp. 231–247, *in* A. K. Minks and P. Harrewijn (eds.). Aphids-Their Biology, Natural Enemies and Control, Vol. B. New York, Elsevier, Amsterdam.

GERLING, D. 1990. Natural enemies of white flies: predators and parasitoids, pp. 147–185, *in* D. Gerling (ed.). Whiteflies: Their Bionomics, Pest Status and Management. Intercept Ltd., Andover.

GILES, K. L., OBRYCKI, J. J., and DEGOOYER, T. A. 1994. Prevalence of predators associated with *Acyrthosiphon pisum* (Homoptera: Aphididae) and *Hypera postica* Gyllenhal (Coleoptera: Curculionidae) during growth of the first crop of alfalfa. *Biol. Cont.* 4:170–177.

HAGEN, K. S. 1987. Nutritional ecology of terrestrial insect predators, pp. 533–577, *in* F. Slansky and J. G. Rodriguez (eds.). Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates. Wiley & Sons, New York.

HARDIE, J., HICK, A. J., HÖLLER, C., MANN, J., and MERRITT, L. 1994. The responses of *Paron* spp. parasitoids to aphid sex pheromone components in the field. *Entomol. Exp. Appl.* 71:95–99.

JOURDAN, H., BARBIER, R., BERNARD, J., and FERRAN, A. 1995. Antennal sensilla and sexual dimorphism of the adult lady beetle *Semiadalia undecimnotata* Schn. (Coleoptera: Coccinellidae). *Int. J. Insect Morphol. Embryol.* 24:307–322.

NAKAMUTA, K. 1991. Aphid alarm pheromone component, (E)-β-farnesene, and local search by a predatory lady beetle, *Coccinella septempunctata bruckii* Mulsant (Coleoptera: Coccinellidae). *Appl. Entomol. Zool.* 26:1–7.

NAULT, L. R., EDWARDS, L. J., and STYER, W. E. 1973. Aphid alarm pheromones: Secretion and reception. *Environ. Entomol.* 2:101–105.

NEW, T. R. 1975. The biology of Chrysopidae and Hemerobiidae (Neuroptera) with reference to their usage as biocontrol agents: a review. *Trans. R. Entomol. Soc. London* 127:115–140.

OBATA, S. 1987. Mechanisms of prey finding in the aphidophagous ladybird beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae). *Entomophaga* 31:303–311.

OBRYCKI, J. J., and KRING, T. J. 1998. Predaceous coccinellidae in biological control. *Annu. Rev. Entomol.* 43:295–321.

PETTERSSON, J. 1970. An aphid sex attractant I. Biological studies. *Entomol. Scand.* 1:63–73.

PHOOFOLO, M. W. 1997. Evaluation of natural enemies of the European corn borer, *Ostrinia nubilalis* (Lepidoptera: Pyralidae). PhD thesis. Iowa State University, Ames, 172 pp.

SPARKS, A. N., CHIANG, H. C., BURKHARDT, C. C., FAIRCHILD, M. L., and WEEKMAN, G. T. 1966. Evaluation of the influence of predation on corn borer populations. *J. Econ. Entomol.* 59:104–107.

TURLINGS, T. C. J., WACKERS, F. L., VET, L. E. M., LEWIS, W. J., and TUMLINSON, J. H. 1992. Learning of host-finding cues by hymenopterous parasitoids, pp. 51–78, *in* A. C. Lewis and D. R. Papaj (eds.). Insect Learning: Ecological and Evolutionary Perspectives. Chapman and Hall, New York.

UDAYAGIRI, S. 1996. Behavioral manipulation of natural enemies: Potential use in insect pest management. *Agric. Zool. Rev.* 7:181–216.

VAN EMDEN, H. F., and HAGEN, K. S. 1976. Olfactory reactions of the green lacewing, *Chrysopa carnea*, to tryptophan and certain breakdown products. *Environ. Entomol.* 5:469–473.