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Semiochemical lures reduce emigration and enhance pest control services in open-field predator augmentation

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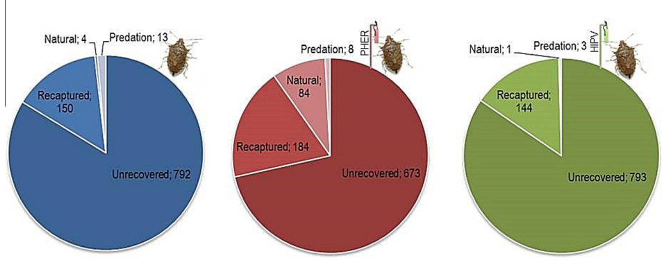
HIGHLIGHTS

- Retention rates of augmented *P. maculiventris* were increased in optimal weather.
- Optimal weather + aggregation pheromone further reduced *P. maculiventris* emigration.
- Semiochemical lures elicited point-source attraction of predators.
- Augmented and wild *P. maculiventris* contributed to pest control services.
- Parasitoids (Diptera and Hymenoptera) were attracted to both pheromone and HIPVs.

GRAPHICAL ABSTRACT

P. maculiventris movement by augmentation manipulation treatment (AUG – blue; AUG + PHER – red; AUG + PHER – green).



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ABSTRACT

Augmentation biocontrol is a commercially viable pest management tactic in enclosed glasshouse environments, but is far less effective in open-field agriculture where newly released enemies rapidly disperse from release sites. We tested the potential for behavior-modifying semiochemicals to increase the retention of mass released predatory stink bugs, *Podisus maculiventris* Say (Hemiptera: Pentatomidae), for enhanced consumption of hornworm caterpillars, *Manduca sexta* L. (Lepidoptera: Sphingidae). To do so, we used controlled-release dispensers to emit the herbivore-induced plant volatile, methyl salicylate (MeSA), or *P. maculiventris* aggregation pheromone from tomato field plots. Overall, we recaptured ca. 17% of released individuals after 36 h. This rate, however, was significantly affected by weather (12% vs. 22% recapture in rainy vs. dry weeks, respectively) and semiochemical deployment, but only under optimal weather conditions (19% vs. 26% recapture in control vs. pheromone plots, respectively, during dry weeks). Further, we detected behavioral responses of wild *P. maculiventris* to semiochemical treatment with 94% of all captured adults (=84 of 89 total) found in pheromone plots. Only 24 of 567 (4%) captured stink bugs tested positive for immunomarking, suggesting that hornworm predation occurred but at a low frequency. Importantly, we documented that sentinel caterpillar prey were depleted by predators at a higher rate in stink bug augmented plots on tomato plants occurring near (<3 m from) the MeSA and pheromone lures. These data empirically demonstrate that both semiochemicals are capable of increasing pest consumption via attraction of *P. maculiventris*. Future work should focus on mechanisms of lure attraction and the long-term consequences of predator development in fields with elevated semiochemical emissions.

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1. Introduction

Augmentation biological control (hereafter, "augmentation") is the practice of mass releasing natural enemies in a pest-infested crop, aimed at obtaining more effective control than that provided by naturally-occurring predators and parasitoids. While this technique has potential application in a wide range of agricultural systems, it has primarily been employed in greenhouses for the management of horticultural pests such as whiteflies, thrips, and mites (Gerling et al., 2001; Gillespie, 1989; van Lenteren et al., 1997; van Lenteren and Woets, 1988). Implementation in open-field agriculture is far less prevalent and frequently unsuccessful when tested. For example, only 15% of experimental field studies effectively reduced pest abundance to target densities, whereas 64% failed (Collier and Van Steenwyk, 2004). Importantly, dispersal of augmented beneficials beyond the targeted area was noted as a central factor underlying the failure of these release programs. Heimpel and Asplen (2011) also highlighted excessive dispersal as a key mechanism driving the failure of inundative biocontrol releases. For example, only 9 lady beetles (*Hippodamia convergens* (Guérin-Méneville)) were recaptured 24 h after releasing 7125 adults into wheat, corn, and alfalfa fields, yielding a recapture rate of merely 0.1% (Kieckhefer and Olsen, 1974). Later attempts released an astounding 2,250,000 individuals and after just 4 days not a single released predator was detected in the field (Kieckhefer and Olsen, 1974). With such poor retention, far more enemies must be purchased than are actually needed to account for loss due to emigration, making augmentation cost ineffective as a pest management tool for the vast majority of crops.

Restricting natural enemy movement can reduce emigration, thereby enhancing the per-capita impact of released individuals on prey. Prior work has mostly emphasized techniques that physically manipulate wings to discourage or prevent flight (e.g., clipping, artificial selection, identification of natural flightless strains), which have proven quite effective (Ferran et al., 1998; Ignoffo et al., 1977; Lommen et al., 2008, 2013; Seko et al., 2008) but also come with ecological and/or physiological costs. Namely, flightless predators have shown reduced survival and fecundity compared with flight-capable individuals (Seko and Miura, 2009). Integrating behavior-modifying semiochemicals with predator or parasitoid releases, however, may decrease the dispersal of augmented beneficials without the associated costs of flightlessness. Two promising candidates include herbivore-induced plant volatiles (HIPVs) and aggregation pheromones.

HIPVs are chemicals released from plants after herbivore feeding damage that are often used by higher trophic level arthropods to locate their prey (Kessler and Baldwin, 2001; Thaler, 1999; Turlings et al., 1990). Recent reviews have stressed the utility of HIPV manipulations in modern biocontrol research (Kaplan, 2012; Khan et al., 2008; Rodriguez-Saona et al., 2012; Turlings and Ton, 2006). However, these perspectives and the existing empirical work exclusively focus on applications of HIPVs as attractants in conservation biocontrol to increase recruitment of naturally-occurring enemies into crop fields (James, 2003; James and Price, 2004; Mallinger et al., 2011; Rodriguez-Saona et al., 2011). HIPVs could serve an analogous role in augmentation by acting as arrestants, decreasing emigration from release sites. To date, no study has tested this hypothesis.

Aggregation pheromones are compounds emitted by male insects that are attractive to conspecifics, including both sexes and multiple life stages (i.e., adults + immatures) (Matthews and Matthews 2010). In pest management, aggregation pheromones are used in attraction–annihilation whereby insecticide-baited pheromone traps are used to lure and kill pests (Lanier, 1990). In comparison, relatively few aggregation pheromones have been identified for beneficial arthropods. The only case in which a natural enemy aggregation pheromone has been used in biocontrol came after the identification and synthesis of the aggregation pheromone from the spined solider bug, *Podisus maculiventris* (Say) (Aldrich et al., 1984). Two companion studies used synthetic pheromone in dispensers bordering the release plot to facilitate the movement of augmented nymphs from their hatching site into pest-infested potato fields (Aldrich and Cantelo, 1999; Sant'Ana et al., 1997). Thus, similar to the mechanisms by which HIPVs function, aggregation pheromones may be useful in increasing natural enemy retention time in an area, as well as recruiting natural populations from adjacent habitats.

We tested the hypothesis that HIPVs and aggregation pheromone reduce emigration of augmented predators from field plots and increase pest consumption in a crop–pest–predator system consisting of tomato, hornworm caterpillars (*Manduca sexta* L.), and the predaceous stink bug, *P. maculiventris*.

2. Materials and methods

2.1. Study system

The tobacco hornworm, *M. sexta*, is a specialist herbivore on solanaceous plants and a common defoliating pest of tomato throughout the United States with tendencies to outbreak in the Northeast and Northern Midwest (Foster and Flood, 2005). Hornworms used in this project derived from a laboratory colony maintained in West Lafayette, Indiana and were reared as neonates on artificial diet until use in field trials (see Section 2.5).

The stink bug, *P. maculiventris*, is a native generalist predator, predominantly consuming lepidopteran and coleopteran larvae, which feeds by piercing prey and sucking their internal fluids via its rostrum. It has shown promise as a biocontrol agent for inundative releases (Biever and Chauvin, 1992a,b; Evans, 1982; Hough-Goldstein, 1998) and is currently the only commercially available predaceous stink bug in North America (Rincon–Vitova Insectaries, Ventura, CA). Adult *P. maculiventris* used in our experiment were maintained in a laboratory colony established with insects from Rincon–Vitova Insectaries and supplemented yearly with field caught individuals from local populations. The colony was maintained at 16:8 LD at 26 °C with bean and tomato plants for water and *ad libitum* mealworms, *Tenebrio molitor* L., as prey.

2.2. Experimental design

Sixteen 100 m^2 field plots, each containing ca. 100 tomato plants (5 rows × 20 plants/row) with >75 m inter-plot spacing, were established during the summer of 2012 on the Meigs Farm at Throckmorton Purdue Agricultural Center (Lafayette, IN, USA). Processing tomato seedlings (RG-611; Red Gold Inc., Elwood, IN, USA) were transplanted from mist-houses into plastic-covered, raised beds in late May. All plots received drip irrigation, fertilizer, and herbicide applications as needed to manage weeds, but insecticides were not used.

Plots were assigned to one of four augmentation/semiochemical treatments in a randomized complete block design, each block replicated four times: (i) *P. maculiventris* release + aggregation pheromone [AUG + PHER]; (ii) *P. maculiventris* release + HIPV [AUG + HIPV]; (iii) *P. maculiventris* release + no semiochemicals [AUG]; and (iv) No *P. maculiventris* release + no semiochemicals [CTRL].

2.3. Semiochemical treatments

The *P. maculiventris* aggregation pheromone was formulated with the three primary components in the following ratio: 7.6% (E)-2-hexenal, 0.4% benzyl alcohol and 92% α-terpineol