

Field observations quantifying attraction of four tortricid moths to high-dosage pheromone dispensers in untreated and pheromone-treated orchards

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Abstract

Oriental responses of four species of feral tortricid moths (Lepidoptera: Tortricidae) to polyethylene tube dispensers of pheromone were observed in a 0.8 ha apple orchard treated with such pheromone dispensers and in an untreated 0.8 ha orchard. Male oblique-banded leafrollers, *Choristoneura rosaceana* (Walker) (mean 7.2 ± 0.4 moths/night during 21 nights), Oriental fruit moths, *Grapholita molesta* (Busck) (mean 10.5 ± 2.1 during 20 evenings), and the redbanded leafrollers, *Argyrotaenia velutinana* (Walker) (mean 2.0 ± 1.1 during 14 nights) were observed approaching within 100 cm of their respective polyethylene-tube pheromone dispensers in the untreated orchard. Furthermore, *C. rosaceana* (mean 2.0 ± 0.7 during 17 nights) and *G. molesta* (mean 1.5 ± 0.4 over 20 evenings) came within 100 cm of their respective polyethylene-tube pheromone dispensers in the pheromone-treated orchard. Most visits lasted less than 10 s, after which the majority of moths departed by flying upwind. In the untreated orchard, the number of *C. rosaceana* observed orienting to polyethylene tube dispensers was greater than the number captured in optimized monitoring traps (1.9 ± 0.4) per night of observation. The numbers of *A. velutinana* (2.0 ± 1.1) or *G. molesta* (10.5 ± 2.1) attracted to polyethylene-tube dispensers in the untreated orchard did not differ statistically from the numbers captured in optimized monitoring traps per night of observation. In the pheromone-treated orchard, the number of *C. rosaceana* (2.0 ± 0.4) or *G. molesta* (1.2 ± 0.2) observed orienting to polyethylene-tube dispensers did not differ statistically from the numbers of male moths of these species captured in optimized monitoring traps per night of observation. No codling moths, *Cydia pomonella* L. were observed orienting to, or landing near, their respective polyethylene-tube dispensers in either the untreated or pheromone-treated orchards, although substantial numbers were captured in monitoring traps per night of observation (6.0 ± 1.7) in the untreated orchard. The attraction of male moths to polyethylene tube dispensers thus occurred in three of the four species observed. These results provide support for the idea that false-plume-following is an important component of the mechanisms mediating communicational disruption in moths by polyethylene-tube dispensers.

Introduction

Pheromone-based mating disruption is an important biorational pest-management tactic for insects relying on long-distance pheromones for mate finding (Cardé & Minks, 1995). However, the effectiveness of this approach has

been variable across species (Reissig et al., 1978; Sanders, 1982; Audemard, 1988). Factors influencing the efficacy of mating disruption treatments may include: the completeness of pheromone blend in a disruption formulation (Minks & Cardé, 1988; Evenden et al., 1999a), high population densities, which increase the competition between calling females and pheromone dispensers (Schmitz et al., 1995; Suckling & Angerelli, 1996; Weissling & Knight, 1996; Knight & Turner, 1999), variability in canopy structure and wind direction, which affects pheromone plume structure (Cardé

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& Minks, 1995), and varying durations of antennal adaptation across species (Stelinski et al., 2003a,b).

Some investigations have attempted to uncover why mating disruption sometimes succeeds and at other times fails (Sanders, 1985; Sanders, 1996; Valeur & Löfstedt, 1996; Cardé et al., 1997; Cardé et al., 1998; Sanders, 1998; Evenden et al., 2000; Stelinski et al., 2004). Such investigations have focused on the behavioral and physiological mechanisms underlying mating disruption. Mechanisms postulated to explain mating disruption have been reviewed by Rothschild (1981), Bartell (1982), and Cardé (1990). They include: camouflage, imbalance of sensory input, false-plume-following, and adaptation and/or habituation.

Our recent research on selected leafroller moth species (Lepidoptera: Tortricidae) have included the physiological (Stelinski et al., 2003a,b,c) and behavioral (Stelinski et al., 2004) differences that may contribute to differences in the effectiveness of mating disruption as a control tactic for these species (Gut et al., 2004). Efforts to disrupt the red-banded leafroller, *Argyrotaenia velutinana* (Walker), using synthetic pheromones have been judged successful (Novak et al., 1978; Roelofs & Novak, 1981; Cardé & Minks, 1995), while lesser successes have been documented for the oblique-banded leafroller, *Choristoneura rosaceana* (Harris) (Reissig et al., 1978; Agnello et al., 1996; Lawson et al., 1996). Studies comparing these two species have revealed a species-specific expression and duration of long-lasting peripheral adaptation following exposure to polyethylene-tube pheromone dispensers used in mating disruption (Stelinski et al., 2003a,b). Specifically, exposure to pheromone induces minutes-long effects on peripheral reception in *C. rosaceana* but not *A. velutinana* (Stelinski et al., 2003a,b) and day-long effects on behavioral responsiveness to pheromone in both *C. rosaceana* and *A. velutinana* (Stelinski et al., 2004).

The next step in this comparative study was to describe the behavioral interactions of these two species with commercially available mating disruption dispensers in orchards. The current communication describes the behavioral observations of four tortricid moth species [*C. rosaceana*, *A. velutinana*, Oriental fruit moth, *Grapholita molesta* (Busck), and codling moth, *Cydia pomonella* (L.)] in close proximity to their mating disruption dispensers in orchards.

Materials and methods

Field observations

This study was conducted between May and September of 2003 at the Trevor Nichols Research Complex (TNRC) of Michigan State University in Fennville, MI. Visual observations were conducted on sunny and calm evenings starting

at 16.30 hours and lasting through to 00.30 hours in two 0.8 ha orchards of 18-year-old Delicious apple trees with ca. 2–3 m canopy heights. Trees were planted on a 3 m within- and 6 m between-row spacing. The orchards were spaced ca. 85 m apart. One orchard was left untreated while the second received treatments of three types of polyethylene-tube pheromone dispensers at recommended label rates (see description below). The pheromone-treated orchard was located downwind of the untreated orchard, based on the prevailing wind direction at the TNRC. The pheromone treatments targeted four species of tortricids known to infest these orchards, viz., *G. molesta*, *C. pomonella*, *A. velutinana*, and *C. rosaceana*. The ‘experimental unit’ in this behavioral study was considered to be the portion of orchard space into which pheromone from a dispenser produced an active space.

Pheromone dispensers

The polyethylene-tube pheromone dispensers used for observations and applied as mating disruption treatments were: (1) Isomate-M Rosso containing 250 mg of 88.5% (*Z*)-8-dodecenyl-acetate, 5.7% (*E*)-8-dodecenyl-acetate, 1.0% *Z*-8-dodecenol, and 4.8% inert ingredients (500 dispensers ha⁻¹) targeting *G. molesta*; (2) Isomate-C Plus containing 205 mg of 53.0% (*E,E*)-8,10-dodecadienol, 29.7% dodecanol, 6.0% tetradecanol, and 11.3% inert ingredients (1000 dispensers ha⁻¹) targeting *C. pomonella*; and (3) Isomate OBLR/PLR Plus containing 274 mg of 93.4% (*Z*)-11-tetradecenyl acetate, 5.1% (*E*)-11-tetradecenyl acetate, and 1.5% (*Z*)-9-tetradecenyl acetate (500 dispensers ha⁻¹) targeting both *C. rosaceana* and *A. velutinana*. All dispensers were hung in trees ca. 1.5–2 m above the ground and in the upper third of the tree canopy. Isomate-M Rosso, Isomate-C Plus, and Isomate-OBLR/PLR dispensers were applied in the orchard on 1 May, 27 May, and 12 June, respectively. After 12 June, all three dispenser types were present concurrently. Dispensers used in field observations were field-aged to match the age of those used for mating disruption.

Observational arena

The observational arena was a 71 cm high, vinyl-covered table measuring 86 × 86 cm. The table top was demarcated with tape in a 10 × 10 cm grid to aid estimation of the proximity of observed moths to a polyethylene-tube pheromone dispenser affixed above the table’s center. An individual pheromone dispenser was twisted onto an apple branch (ca. 50 cm long, 1.5 cm diameter) removed from a tree in the experimental plot. The apple branch was then affixed horizontally and approximately 32 cm above the tabletop to a steel ring-stand. The stand was positioned in the center of the observational table. Wind direction at the

observational arena was concurrently monitored by the observer noting deflections of a 20 cm piece of flagging tape hanging from a second ring-stand placed adjacent to the one holding the apple branch with the pheromone dispenser. Detailed weather data, including wind speed and direction, were recorded by a weather station on the TNRC, 80 m from the observational arena (Michigan Automated Weather Network, <http://www.agweather.geo.msu.edu/mawn>). Wind speeds during observations varied from ca. 0.13 to 2.2 m s⁻¹. The observational arena was set up in openings created by missing trees within tree rows at two, four, or six rows interior from the border row of each plot; the specific site of the observational arena was randomly rotated among five locations nightly. The tree spacing and size described above was that of tightly planted, small trees such that the gaps created by missing trees were less than 3 m³. Our aim was to insert the arenas into such small gaps, surrounded by the foliage of neighboring trees, so as to mimic the position of a dispenser within an actual tree, rather than conducting observations within the corridor between tree rows. The design of our arena allowed for the conductance of detailed quantifications of moth behaviors that may have been difficult to observe directly within trees.

Observed events were spoken into a hand-held micro-cassette audio recorder by an investigator sitting ca. 0.8 m from the observational arena. Data recorded included: anemotactic orientations to the dispenser, closest approach to the dispenser, landings at the observation arena, time during the diel period, and duration of visits. Observations after dusk were assisted by night-vision goggles (Rigel 3100, DeWitt, IA) with a 40° field of view, 0.5–200 m viewing distance, and resolution of 28 lines/mm. In rare cases with little sky light (ca. below 0.01 lux), an infrared illuminator mounted on the goggles was activated to improve resolution. In preliminary lab tests, this illuminator did not appear to affect moth behavior and no differences were noted in moth behavior in the field whether it was on or off. At peak moth activity during the diel cycle (see Results), multiple moth visits occasionally occurred simultaneously; however, we estimate that more than 90% of all moth visits were documented.

Concurrent with the observations, the attraction of male moths to sex pheromone was monitored using pheromone traps (LPD Scenurian Guardpost, Suterra, Bend, OR) placed in both the untreated and pheromone-treated orchards. Traps were baited with monitoring lures containing pheromone blends attractive to each species. For *A. velutinana*, rubber septa were loaded with 0.93 mg (*Z*)- and 0.07 mg (*E*)-11-tetradecenyl acetates (93 : 7 ratio of *Z*:*E*) and 2.0 mg dodecyl acetate (Roelofs et al., 1975). For *C. rosaceana*, rubber septa were loaded with 0.485 mg of

(*Z*)- and 0.015 mg (*E*)-11-tetradecenyl acetates (92.2 : 3.0 ratio of *Z*:*E*) and 0.026 mg of (*Z*)-11-tetradecenol (Hill & Roelofs, 1979). For *C. pomonella*, septa were loaded with 1 mg of (*E,E*)-8,10-dodecadien-1-ol. Finally, for *G. molesta*, septa were loaded with 3 µg of (*Z*)-8-dodecenyl acetate: (*E*)-8-dodecenyl acetate: *Z*-8-dodecenol in a 100 : 6 : 10 blend. The pheromone blend solutions used to load rubber septa were prepared in HPLC grade hexane and stored at -18 °C. Three traps were deployed in each plot per species; traps were maintained ca. 50 m from the observation arena. They were hung ca. 1.5–2 m above ground level in the upper third of the tree canopy. New pheromone lures were deployed every 2 weeks for each trap. Moths captured in traps were counted and removed following each observational period. Monitoring traps were deployed only when direct observations of moth attraction to tube-dispensers were conducted.

For each species, direct observations were carried out between two and five times per week during their respective adult generations. The first and second generations of *G. molesta* were observed 5 May–9 June and 7 June–2 September, respectively. For *G. molesta*, observations were made on 20 evenings in the untreated orchard and on 20 evenings in the pheromone-treated orchard. The first and second generations of *C. rosaceana* were observed 17 June–2 September and the second and third generations of *A. velutinana* were observed 30 June–8 September. For *C. rosaceana* and *A. velutinana*, observations were made on 21 and 14 evenings, respectively, in the untreated orchard and on 17 and 14 separate evenings, respectively, in the pheromone-treated orchard. The first and second generations of *C. pomonella* were captured in traps on 3 June–1 September. For *C. pomonella*, observations were made on 15 evenings in the untreated orchard and on 15 separate evenings in the pheromone-treated orchard.

Statistical analyses

Comparisons of mean moth catches in traps and mean numbers of moths observed throughout the entire season at the observational arena in untreated vs. pheromone-treated orchards were accomplished with analysis of variance (ANOVA) and Fisher-protected least significant difference (LSD) multiple comparison procedures (SAS Institute, 2000). Comparisons of mean moth catches in traps vs. numbers of moths observed at the observational arena per night were carried out using a two-sided (tailed) *t*-test. Because no *C. pomonella* were observed in either pheromone-treated or untreated orchards and no *A. velutinana* were observed in the pheromone-treated orchard, these data were excluded from the analysis. All data were square-root transformed [(*x* + 0.5)^{1/2}] before analysis. In all cases, the significance level was set at $\alpha < 0.05$.

Results

Number of moths observed at polyethylene-tube dispensers and in monitoring traps

Over the course of their respective flight periods, *C. rosaceana*, *G. molesta*, and *A. velutinana* were consistently attracted to within 100 cm of their respective polyethylene-tube pheromone dispensers in the untreated orchard (Table 1). Likewise, *C. rosaceana* and *G. molesta* came within 100 cm of their respective dispensers in the pheromone-treated orchard (Table 1).

Significantly more *C. rosaceana* and *G. molesta* approached their respective pheromone dispensers in the untreated orchard than in the pheromone-treated orchard (Table 1). In addition, *A. velutinana* approached their pheromone dispensers only in the untreated orchard (Table 1). In contrast, *C. pomonella* were not observed approaching their dispensers in either the untreated or pheromone-treated orchards (Table 1). However, *C. pomonella* were captured in optimized monitoring traps in both orchards (Table 1).

The mean number of *C. rosaceana* approaching pheromone dispensers per night in the untreated orchard was significantly ($P < 0.05$) greater than the mean number captured in monitoring traps (Table 1). However, the mean number of *A. velutinana* or *G. molesta* approaching pheromone dispensers per night in the untreated orchard was not statistically ($P > 0.05$) different from the mean number captured in the monitoring traps (Table 1).

In the pheromone-treated orchard, the mean number of *C. rosaceana* or *G. molesta* approaching pheromone dispensers was not statistically ($P > 0.05$) different from the mean number captured in monitoring traps (Table 1).

Duration of stay and proximity to ropes

Nearly all *C. rosaceana* observed were attracted to within 100 cm of their polyethylene tube dispenser in both untreated and pheromone-treated orchards, and a third of these approached within 10 cm of the it (Figure 1A). However, no individuals of this species were observed landing at the observational arena. The majority of *C. rosaceana* left the observational arena within 10 s of initial sighting in both untreated and pheromone-treated orchards (Figure 1B).

All of the *G. molesta* observed approached within 100 cm of their dispenser (Figure 1C). Of the four moth species observed, *G. molesta* was the only one to sometimes land at the observational arena. Specifically, 95 (out of 220 total) and three (out of 22 total) *G. molesta* landed at the observational arena in the untreated and pheromone-treated orchards, respectively. The *G. molesta* moths that landed at the arena wing-fanned vigorously and walked rapidly; they remained in motion for the duration of their stay. A total of 14 *G. molesta* landed on the branch upon which a polyethylene tube dispenser had been hung, and four directly contacted the dispenser. The majority of *G. molesta* observed was attracted within 20–60 cm of their dispenser

Species followed by treatment pairs	Mean number \pm SEM of moths captured in traps per night		Mean number \pm SEM of observed visits to dispensers per night
<i>Choristoneura rosaceana</i> (21 nights of observation)			
Untreated plot	1.9 \pm 0.4a ^a	*	7.2 \pm 0.4a
Pheromone-treated plot	1.2 \pm 0.2a	ns	1.95 \pm 0.7b
<i>Argyrotaenia velutinana</i> (14 nights of observation)			
Untreated plot	6.3 \pm 1.0	ns	2.0 \pm 1.1
Pheromone-treated plot	0.0 \pm 0.0		0.0 \pm 0.0
<i>Grapholita molesta</i> (20 evenings of observation)			
Untreated plot	8.5 \pm 1.0a	ns	10.5 \pm 2.1a
Pheromone-treated plot	0.3 \pm 0.1b	ns	1.53 \pm 0.4b
<i>Cydia pomonella</i> (15 evenings of observation)			
Untreated plot	6.0 \pm 1.7a		0.0 \pm 0.0
Pheromone-treated plot	0.09 \pm 0.01b		0.0 \pm 0.0

Table 1 Mean \pm SEM number of moths captured in traps and observed visiting polyethylene-tube dispensers per night

^aPairs of means in the same column followed by the same letter are not significantly different ($P < 0.05$, ANOVA followed by LSD test). Paired values within rows marked with an asterisk are significantly different ($P < 0.05$, t-test) and ns indicates lack of significance.

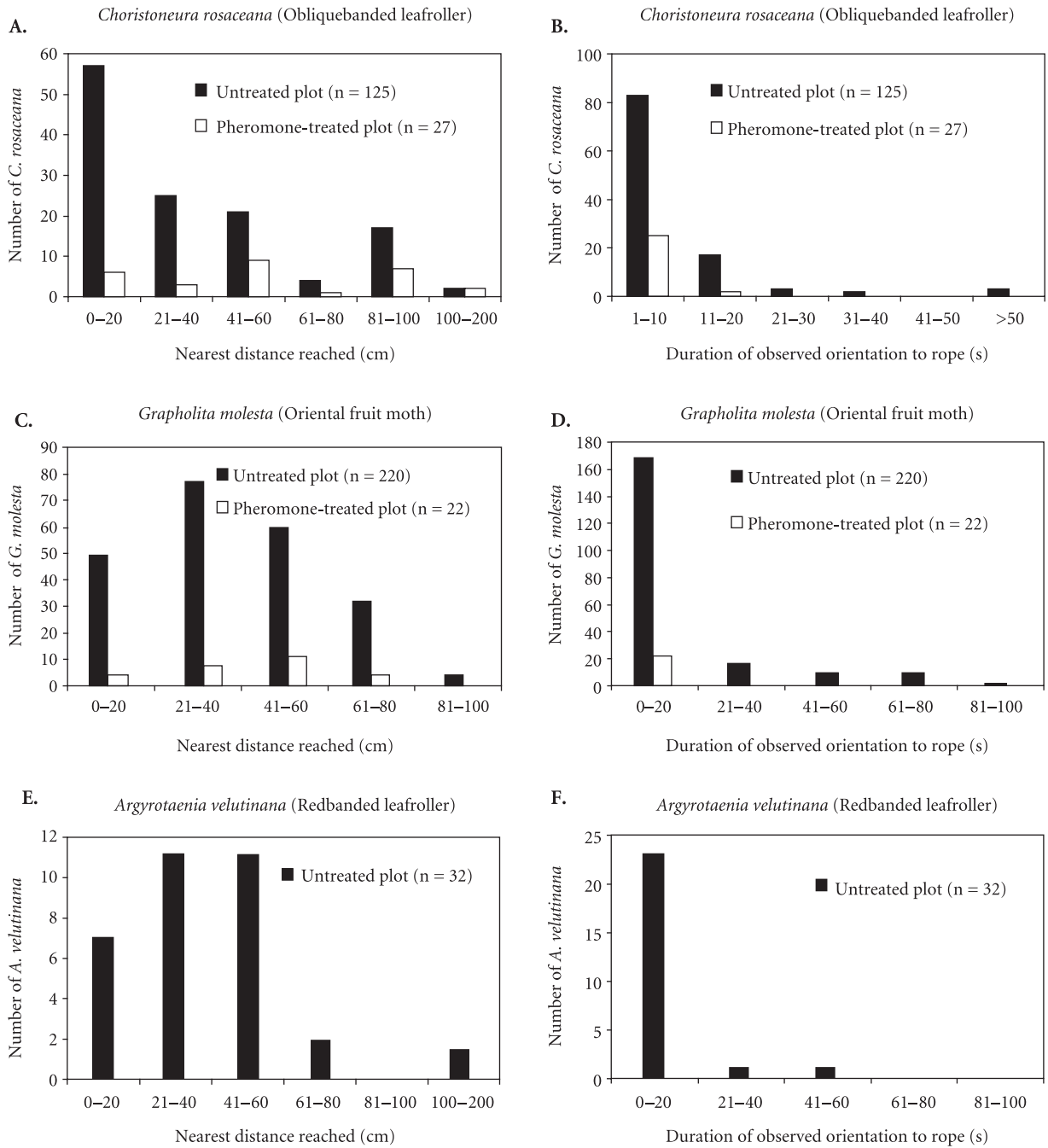


Figure 1 (A) Nearest distance reached by feral oblique-banded leafrollers, *Choristoneura rosaceana*, attracted to Isomate OBLR/PLR dispensers in an untreated or pheromone-treated orchard. (B) Duration of stay of *C. rosaceana* observed in close proximity to Isomate OBLR/PLR dispensers. (C) Nearest distance reached by feral Oriental fruit moths, *Grapholita molesta*, attracted to Isomate-M Rosso dispensers in an untreated or pheromone-treated orchard. (D) Duration of stay of *G. molesta* observed in close proximity to Isomate-M Rosso dispensers. (E) Nearest distance reached by feral redbanded leafrollers, *Argyrotaenia velutinana*, attracted to Isomate OBLR/PLR dispensers in an untreated or pheromone-treated orchard. (F) Duration of stay of *A. velutinana* observed in close proximity to Isomate OBLR/PLR dispensers. No *A. velutinana* were observed approaching Isomate OBLR/PLR dispensers in the pheromone-treated orchard. Note the different scales on the y-axes.

(Figure 1C) and left within 10 s in both untreated and pheromone-treated orchards (Figure 1D). The three *G. molesta* landing at the observational arena in the pheromone-treated orchard left within 20 s.

All *A. velutinana* approached within 70 cm of the dispenser in the untreated orchard (Figure 1E). The majority of *A. velutinana* observed in the untreated orchard left the observational arena within 10 s of initial sighting (Figure 1F). No *A. velutinana* were observed approaching their dispensers in the pheromone-treated orchard. In addition, no individuals of this species were observed landing at the observational arena in the untreated orchard.

Grapholita molesta oriented toward their respective polyethylene-tube pheromone dispensers placed at the observational arena from heights below that of the table (ca. 0.5–0.8 m above ground level). In contrast, *C. rosaceana* and *A. velutinana* oriented toward their respective polyethylene-tube dispensers from heights above the table (ca. 2–3 m above ground level). Upon leaving the arena, the majority of moths from all species flew upwind.

Activity period

Choristoneura rosaceana (17 June–2 September) and *A. velutinana* (30 June–8 September) were observed at the observational arena and captured in traps after sunset between 21.45 and 00.15 hours. During their first generation of adult flight (5 May–9 June), *G. molesta* were observed at the observational arena and captured in traps before sunset between 16.40 and 20.15 hours. The activity of subsequent generations occurred later, between 19.30 and 21.30 hours (before sunset) in July through September. The above-described diel rhythms of responsiveness of *C. rosaceana* and *G. molesta* to polyethylene-tube pheromone dispensers were identical in both the untreated and pheromone-treated orchards. *Cydia pomonella* were captured in traps after sunset between 21.30 and 23.30 hours in June through late August.

Discussion

Throughout their respective adult generations, *C. rosaceana*, *G. molesta*, and *A. velutinana* were consistently attracted within 100 cm of their respective high-release, polyethylene-tube pheromone dispensers in an untreated apple orchard. *Choristoneura rosaceana* and *G. molesta* were also frequently observed orienting to their respective polyethylene-tube dispensers in a comparison orchard treated with standard densities (ca. 1 tree⁻¹) of such dispensers for mating disruption. Using field wind tunnels, Cardé et al. (1997, 1998) observed the behavioral interactions of laboratory-reared pink bollworm moths, *Pectinophora gossypiella*, with high-release pheromone disruption dispensers targeting

this species (PBW-Ropes, Shin-Etsu, Tokyo, Japan). In that study, released *P. gossypiella* also approached and often contacted the dispensers. The majority of these males left the dispensers within a few minutes and many walked while wing-fanning on cotton foliage nearby. Our data corroborate the Cardé et al. (1998) findings documenting that moths approach and interact with high-release polyethylene-tube dispensers.

The attraction of male moths to polyethylene tube dispensers occurred in three of the four species observed in this study. This finding suggests that false-plume-following may play an important role in mating disruption using such dispensers. Polyethylene tube dispensers attracted approximately equal numbers of *A. velutinana*, *G. molesta*, and *C. rosaceana* as were captured in traps baited with optimally tuned monitoring lures in an untreated orchard. If the nightly observations made at a single polyethylene tube dispenser in this study reflect what is taking place at the majority of dispensers in a treated plot, then direct competition by sources of sex-attractant would decrease the time available for males to find females. However, under high population densities of calling females, such competition may be insufficient to prevent males from eventually finding and mating with a female after orientations to synthetic pheromone dispensers. Therefore, high population pressures may necessitate that the management strategy invoke other mechanisms such as camouflaging of female plumes.

Additionally, false-plume-following to dispensers may, in some cases, induce neurophysiological effects due to high-dosage pheromone exposures (Cardé et al., 1997, 1998). Consequential neurophysiologically mediated effects on the behavior of moths following exposures to pheromone have been documented in the laboratory (Bartell & Lawrence, 1977; Linn & Roelofs, 1981; Sanders, 1985, 1996; Figueredo & Baker, 1992; Anderson et al., 2003; Stelinski et al., 2004) at dosages similar to those occurring adjacent to polyethylene tube dispensers. The most recent measures of average air-borne pheromone concentrations achieved at sites roughly equidistant from polyethylene tube dispensers deployed at recommended densities were $1.7 \pm 15 \text{ ng m}^{-3}$ of *P. gossypiella* pheromone and $1.9 \pm 0.4 \text{ ng m}^{-3}$ of *C. pomonella* pheromone (Koch et al., 1997; Koch et al., 2002). However, studies with various moth species reveal that the concentrations of pheromone necessary to reduce positive behavioral responsiveness or peripheral sensitivity are substantially greater than those that can be achieved in an average volume of air in a crop under mating disruption. For example, the confinement of *Lobesia botrana* in vineyard plots treated with polyethylene-tube dispensers (1 dispenser per 5 m², each dispenser containing 500 mg of (*E,Z*)-7,9-dodecadienyl acetate) for 8 h did not affect the

moths' ability to subsequently find pheromone point-sources in untreated plots. Moreover, a reduction of behavioral responsiveness to pheromone was only induced when exposure concentrations in the laboratory reached $4 \mu\text{g l}^{-1}$ of pheromone (Schmitz et al., 1997). Furthermore, the reduction of behavioral responsiveness to pheromone for male *G. molesta* only occurred after 1 h of laboratory exposure to its pheromone at a concentration of $65 \mu\text{g m}^{-3}$ (3200 female equivalents) (Rumbo & Vickers, 1997). In addition, EAG measurements revealed that long-term effects on peripheral sensitivity in *C. rosaceana* only occurred after minutes-long confinement in the laboratory at concentrations of pheromone of at least 1 ng ml^{-1} or in the field only when confined for 24 h within a few cm of Isomate OBLR/PLR dispensers (Stelinski et al., 2003b). Collectively, current data suggest that average air-borne concentrations of pheromone in field plots treated with mating disruption dispensers are insufficient to reduce positive behavioral responses to pheromone. Therefore, we suggest that neurophysiological modifications, thought to be important contributors to mating disruption, are mainly induced when moths come close to high-release devices. Thus, it may be critically important that mating disruption formulations or dispensers attract moths within centimeters of the source. The data presented here establish that at least three species of tortricids do come within a few centimeters of their respective polyethylene tube dispensers.

In addition to long-term neurophysiological modifications, real-time effects on peripheral sensitivity may influence moth behavior as they approach polyethylene tube dispensers in the field. Kuenen & Baker (1981) documented that moths, challenged by continuous exposure to pheromone in the laboratory, experienced instantaneous antennal adaptation as measured by EAGs. However, no long-term effects were found after the removal of moths from pheromone. Therefore, it is possible that peripheral adaptation may be induced in moths orienting along plumes generated by polyethylene tube dispensers. Interestingly, tortricid moths, such as *G. molesta*, are capable of orienting along the edges of concentrated pheromone plumes or walls of pheromone in wind tunnels (Kennedy et al., 1981; Willis & Baker, 1984). Such documented behaviors in wind tunnels may partially explain how tortricids in our study were able to orient along plumes from high-dosage polyethylene tube dispensers.

The exception to the general pattern of male moth attraction to polyethylene-tube dispensers was that not a single *C. pomonella* was observed orienting to or landing near their dispensers throughout the entire season in either the untreated or pheromone-treated orchards. However, *C. pomonella* has been documented to closely approach an

earlier version of commercial polyethylene tube dispensers (Isomate-C, containing 180 mg of 51.8% of (*E,E*)-8,10-dodecadienol, 29.1% dodecanol, 6.0% tetradecanol, and 13.1% inert ingredients) (Barrett, 1995) that contained 25 mg less total pheromone than the dispensers used in the current study. The finding that *C. pomonella* did not approach Isomate-C Plus dispensers in this study was not due to low moth population densities, given the high captures of male *C. pomonella* in the monitoring traps (Table 1) and in orchards directly surrounding ours (data available online: <http://www.maes.msu.edu/tncrc/>). Despite the lack of observed visits to Isomate-C Plus dispensers by *C. pomonella* in both the untreated or pheromone-treated orchard, *C. pomonella* captures in monitoring traps were nearly completely inhibited by the pheromone treatment (Table 1).

We can only speculate as to why the Isomate-C Plus dispensers used in the current study did not elicit close visits. It is possible that *C. pomonella* locked onto plumes from these high-release pheromone dispensers, but became arrested (Baker & Cardé, 1979) or exited those plumes at a distance downwind of the observational arena before such behavior could be noted. Whether lower-release, point-source dispensers could attract *C. pomonella* closer than high release counterparts should be investigated further (Charmillot, 1990). Alternatively, it is plausible that the disruption of *C. pomonella* orientation to traps occurred through a different mechanism, e.g., camouflage.

It is also possible that we did not see *C. pomonella* approach the dispensers in the observational arena because they may have been positioned too low with respect to this species' normal residence within the tree canopy. Dispensers at the observational arena were positioned ca. 1.0 m above ground level amongst trees averaging 2 m canopy heights. *Cydia pomonella* have been reported to occur primarily in the upper third of the tree canopy (Rothschild, 1982) and recommendations for the placement of monitoring traps have also been set within the upper third of the canopy (Riedl et al., 1986), or at 'mid-canopy' height (Gut & Brunner, 1994). Thus, further observations of field-deployed Isomate-C Plus dispensers at varying heights above 1.0 m must be conducted before it can be concluded that *C. pomonella* never approach them closely.

Witzgall et al. (1999) also observed behaviors of *C. pomonella* in orchards treated with pheromone. The dispensers used were either resin-treated cellulose flakes or polyethylene tubes (similar to those in the current study) containing codlemone (*E8,E10*-12OH; OH), codlemone acetate (*E8,E10*-12Ac; Ac), or a blend of these two components. Overall, more male *C. pomonella* were observed flying in pheromone-treated orchards compared with untreated controls, implying that male *C. pomonella* were

attracted to the treated orchards. However, close-range attraction to dispensers, as was observed for *C. rosaceana*, *G. molesta*, or *A. velutinana* in this study, was rarely observed for *C. pomonella*. Moreover, Witzgall et al. (1999) observed an approximately equal attraction of male *C. pomonella* to dispensers releasing codlemone as to dispensers releasing both codlemone and the behavioral antagonist, codlemone acetate (Hathaway et al., 1974; Witzgall et al., 1997). Furthermore, they observed an increased attraction to dispensers releasing codlemone in the presence of dispensers containing codlemone acetate. These authors postulated that adaptation or habituation might explain the observed attractiveness of dispensers releasing the behavioral antagonist, codlemone acetate. In addition, they concluded that using blends of pheromonal attractants and antagonists may improve the disruption of *C. pomonella*, as such blends may reduce the chance of long-range attraction of male *C. pomonella* to treated orchards and concurrently induce increased close-range responsiveness to pheromone dispensers.

Interestingly, we also observed significant attraction of male *C. rosaceana* to Isomate OBLR/PLR dispensers in this study and in a recent wind tunnel investigation (Stelinski et al., 2004), even though they contained the behavioral antagonist (*Z*)-9-tetradecenyl acetate (Evenden et al., 1999c). Evenden et al. (1999c) found that the use of dispensers containing a 1:1 mixture of (*Z*)-9-tetradecenyl acetate and the four-component western *C. rosaceana* pheromone (Vakenti et al., 1988) achieved levels of orientational disruption to virgin females (>83%), in small-plot trials, that were approximately equal to that achieved with dispensers containing the pheromone alone. Evenden et al. (1999a,b,c) concluded that mating disruption was unlikely to be mediated by false-plume-following and more likely to be mediated by camouflage or receptor adaptation, given that dispensers with incomplete blends or containing a behavioral antagonist were not less effective than those containing multicomponent, attractive blends. The results of the current study caution that direct behavioral observations are required before inferentially ruling out the importance of false-plume-following, because of the presence of a compound that in different circumstances performed as an antagonist. If false-plume-following is an important mechanism mediating the mating disruption of *C. rosaceana*, then perhaps the addition of this antagonist to currently marketed dispensers for mating disruption has made them less effective. More work needs to be conducted to establish whether the addition of this antagonist to dispensers influences the level of mating disruption for *C. rosaceana* in the field.

An improved understanding of the general mechanisms underlying mating disruption among pest species should

help pest managers to improve the efficacy and practicality of this management tactic. The comparative approach taken here, where multiple species are studied in a common habitat, proved valuable given the behavioral differences uncovered between species. Although some investigators have stressed the difficulty in conducting direct visual observations of male moths responding to pheromone sources under authentic field conditions, we found this indeed possible. Moreover, the data produced are useful in elucidating the mechanisms of pheromone disruption as they occur in the field.

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