Occurrence and Duration of Long-Lasting Peripheral Adaptation Among Males of Three Species of Economically Important Tortricid Moths

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ABSTRACT Electroantennograms (EAGs) of *Cydia pomonella* (L.), *Pandemis pyrusana* Kearfott, and *Grapholita molesta* (Busck) documented the presence and duration of long-lasting peripheral adaptation after pheromone preexposure. Moths of each species were preexposed for 1 h to varying dosages (100 ng–100 mg) of the major components of their respective pheromone blends in 1-liter Teflon containers with constant throughput of air. EAGs were performed on all insects 1 min after preexposure and at several subsequent intervals up to 120 min after exposure. Long-lasting peripheral adaptation was recorded by EAG after pheromone preexposure over a range of pheromone dosages in both *C. pomonella* (100 μg–10 mg) and *P. pyrusana* (100 ng–100 mg). This reduction in EAG responsiveness lasted ≈60 and 10 min, respectively, for these two species. For *G. molesta*, a reduction in EAG responsiveness occurred only after 1 h of exposure to the highest dosage of pheromone tested (100 mg). Recovery from adaptation was also rapid in this species: EAGs were significantly reduced to all applied stimulus dosages only at 1-min postexposure. There was substantial variation in the prevalence and duration of decreased EAG responsiveness across the species investigated. However, where long-lasting adaptation was described, the phenomenon lasted ≤60 min. In addition, long-lasting adaptation was induced after prolonged exposures at estimated airborne concentrations of pheromone in the range of nanograms per milliliter, which are much higher than the pheromone concentrations in field plots treated with synthetic pheromone dispensers. Long-lasting peripheral adaptation after pheromone preexposure does not seem to be an important contributor to mating disruption.

KEY WORDS long-lasting adaptation, electroantennogram, *Grapholita molesta*, *Cydia pomonella*, *Pandemis pyrusana*

PHEROMONE-BASED MATING DISRUPTION IS an important biorational alternative to insecticides for controlling lepidopteran pests and has been under development for more than three decades (Cardé and Minks 1995, Gut et al. 2004). Mating disruption is achieved by the release of synthetic pheromones into a crop canopy to disrupt pheromone-mediated mate-finding behaviors. Various mechanisms have been proposed to explain how mating disruption works (Rothchild 1981, Bartell 1982, Cardé 1990). In no specific order, synthetic pheromones are thought to camouflage natural, female-released plumes; act as false trails for searching males; cause an imbalance of sensory input; or desensitize males to pheromone through peripheral sensory adaptation or central nervous system habituation. These mechanisms are thought not to be mutually exclusive (Cardé et al. 1998).

A plethora of studies have been conducted examining the possible mechanisms of mating disruption (Sanders 1982, 1985, 1996, 1998; Valeur and Löfstedt 1996; Mafra-Neto and Baker 1996; Cardé et al. 1998; Evenden et al. 1999a, b, c, 2000; Stelinski et al. 2004, 2005). However, progress has been modest in distinguishing whether a certain mechanism is of greater importance than others. Furthermore, it has proven difficult to falsify the importance of any of the mechanisms mentioned above. Delineating the primary versus secondary mechanism(s) will aid in the development of pheromone technologies for practical use. The likelihood of effectiveness for a pheromone product is enhanced by knowing how it achieves mating disruption in the field.

Continuous and pulsed exposure to pheromone decreases behavior and electrophysiological responsiveness in many moth species (Bartell and Roelofs 1973; Bartell and Lawrence 1976a, b, c; Linn and Roelofs 1981; Kuenen and Baker 1981; Sanders 1985; Rumbo and Vickers 1997; Schmitz et al. 1997; Daly and Figueredo 2000). Typically, this effect, termed adaptation, is dosage-dependent and reversible. In addition, a form of "long-lasting" peripheral adaptation has been described for *Choristoneura rosaceana* (Harris) (Stelinski et al. 2003a, b) that is similar in duration to the adaptation described for *Antheraea polyphemus*

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(Cramer) by Kaissling (1986). Specifically, preexposure of male *C. rosaceana* to the major component of its pheromone blend at concentrations ranging from 1 to 56 ng/ml for durations of 15 or 60 min reduced subsequent EAG responses for up to 11 min postexposure. Most recently, evidence for an even longer lasting variant of this adaptation has been documented for *Cydia pomonella* (L.) (Judd et al. 2005). Ten- and 30-min preexposures of *C. pomonella* to its major pheromone component at ≈35 ng/ml reduced EAG responses for >1 h. However, not all tortricid moth species exhibit long-lasting adaptation (LLA). *Argyrotaenia velutinana* (Walker) retains normal EAG responses after pheromone preexposures that induce long-lasting adaptation in *C. rosaceana* (Stelinski et al. 2003a). Thus, significant variation exists across species.

With respect to mating disruption, the question becomes, is long-lasting adaptation an important contributing factor? If so, mating disruption technologies could be tailored to exploit this phenomenon by maximizing the pheromone exposure dosage male moths receive in the field. However, falsifying the role of long-lasting adaptation in mating disruption would help researchers and engineers focus on mechanisms of greater significance. To investigate whether long-lasting adaptation is an important contributing factor to mating disruption, we sought to determine whether it is prevalent among multiple pest moth species and whether it can be induced at pheromone concentrations achieved in the field. The objective of this study was to document the presence and duration of long-lasting peripheral adaptation after pheromone preexposure of varying intensity in three tortricid pests of economic importance: *C. pomonella, Pandemis pyrusana* Kearfott, and *Grapholita molesta* (Busck).

Materials and Methods

Insect Colonies. *C. pomonella* and *G. molesta* were obtained from 1- and 2-yr-old laboratory colonies, respectively, originally collected as larvae from apple orchards in southwestern Michigan. *P. pyrusana* were obtained from a colony established in 1990 from a commercial apple orchard in Yakima, WA (J. Brunner, Washington State University). *P. pyrusana* collected from an untreated apple orchard in Wenatchee, WA, were added to this colony in 2000 and 2003. Each species was reared at 24°C on pinto bean diet (Shorey and Hale 1965) under a photoperiod of 16:8 (L:D) h. Male pupae of each species were segregated in 1-liter plastic cages and provided with 5% sucrose solution.

Electroantennograms (EAGs). The EAG system and test protocols were identical to those described in Stelinski et al. (2003a, b). Briefly, our EAG system consisted of a data acquisition interface board (Type IDAC-02) and universal single ended probe (Type PRS-1) from Syntech (Hilversum, The Netherlands). The recording and indifferent electrodes consisted of silver-coated wire in glass micropipettes (10-μl microhematocrit capillary tubes) containing 0.5 M KCl. Male insects of each species were 2–4 d old when used for electroantennograms. EAGs measured the maximum amplitude of depolarization elicited by the applied stimulus cartridge and were conducted on intact antennae of live insect preparations.

Chemicals and Stimulus Delivery. The major pheromone components of each species were used as EAG stimuli and as preexposure treatments in adaptation experiments. For experiments with *C. pomonella*, (*E,E*)-8,10-dodecadien-1-ol (99% isomeric and chemical purity) was obtained from Bedoukian Co. (Danbury, CT). For experiments with *P. pyrusana* and *G. molesta*, (Z)-11-tetradecenyl acetate [96.1% (Z)-11-tetradecenyl acetate and 3.9% (*E*)-11-tetradecenyl acetate] and (Z)-8-dodecen-1-yl-acetate (99% isomeric and chemical purity), respectively, were obtained from Shin Etsu (Tokyo, Japan). Chemical purities were confirmed with gas chromatography. Stimulus cartridges used to deliver pheromone to insect antennae for EAG recordings were prepared according to the protocol detailed in Stelinski et al. (2003a, b). Briefly, various concentrations (Figs. 1 and 2) of each pheromone in hexane (20-μl total solution) were pipetted onto 1.4 by 0.5-cm strips of Whatman No. 1 filter paper. After 5 min in a fume hood for solvent evaporation, treated strips were inserted into disposable glass Pasteur pipettes. Stimulus puffs (1 ml) were generated through the cartridges with a clean hand-held 20-ml glass syringe connected to the pipettes with a 1-cm piece of Tygon tubing.

Effect of Pheromone Preexposure Dosage on EAG Responses. Moths of each species were preexposed to pheromone by using adaptation chambers (Stelinski et al. 2003a, b). Briefly, these chambers were cylindrical, 1-liter Teflon containers (Jensen, Coral Springs, FL) equipped with two 64-mm ports in their lids. Glass inlets and outlets were affixed to the lids allowing pressurized air that had been filtered through carbon to pass through the chambers at 30 ml/min. Chambers were divided with wire mesh such that insects were confined in upper halves, whereas one 2-cm-diameter by 0.5-cm-deep stainless steel planchette loaded with a given dosage of pheromone was placed in the lower half. The highest dosage of pheromone tested for each species was 100 μl of neat pheromone in the planchette. Successively lower dosages were achieved by serial dilutions in mineral oil (Aldrich, Milwaukee, WI); pheromone loadings ranged in decade steps from 100 ng to 100 mg. Chambers always equilibrated for 60 min before insertion of insects. Thirteen males of each species were assayed 1 min after 60 min of preexposure to each pheromone concentration. The control treatment consisted of moths ($n = 13$) preexposed in chambers to mineral oil only. Moths were preexposed individually and treatments were alternated at random.

Recovery from Long-Lasting Adaptation. EAGs were performed on 10–13 males of each species before confinement in adaptation chambers for 60 min of continuous pheromone exposure at the 100-mg

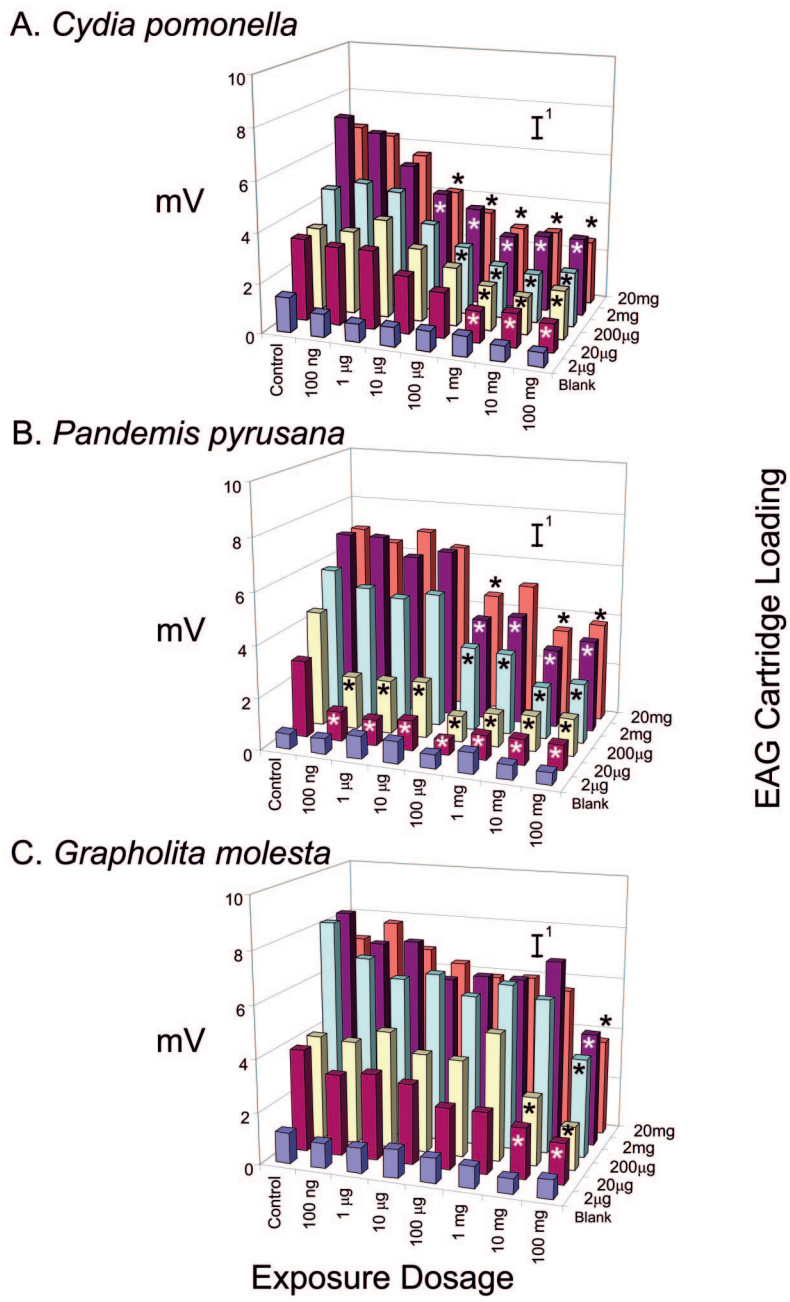

Fig. 1. Effect of 60 min of confinement of (A) *C. pomonella*, (B) *P. pyrusana*, and (C) *G. molesta* ($n = 13$ moths per treatment) in adaptation chambers with various pheromone-loading dosages. Bars with * indicate significant ($P < 0.05$) decrease relative to the control response. [1]Average standard error of the mean for EAG amplitude across all treatments.

pheromone dosage. After exposure, moths were removed from adaptation chambers and placed into pheromone-free air within 1-liter plastic containers. EAGs were performed on all insects 1 min after preexposure and at several subsequent intervals up to 120 min (Fig. 2).

Statistical Analysis. Data collected when testing the effect of preexposure dosage were subjected to analysis of variance (ANOVA), and differences in pairs of means were separated using Tukey's multiple comparisons test (SAS Institute 2000). Data collected when testing the effect of recovery interval were subjected to repeated measures ANOVA, and differences in pairs of means over time were separated by Tukey's test. In all cases, the significance level was $\alpha < 0.05$.

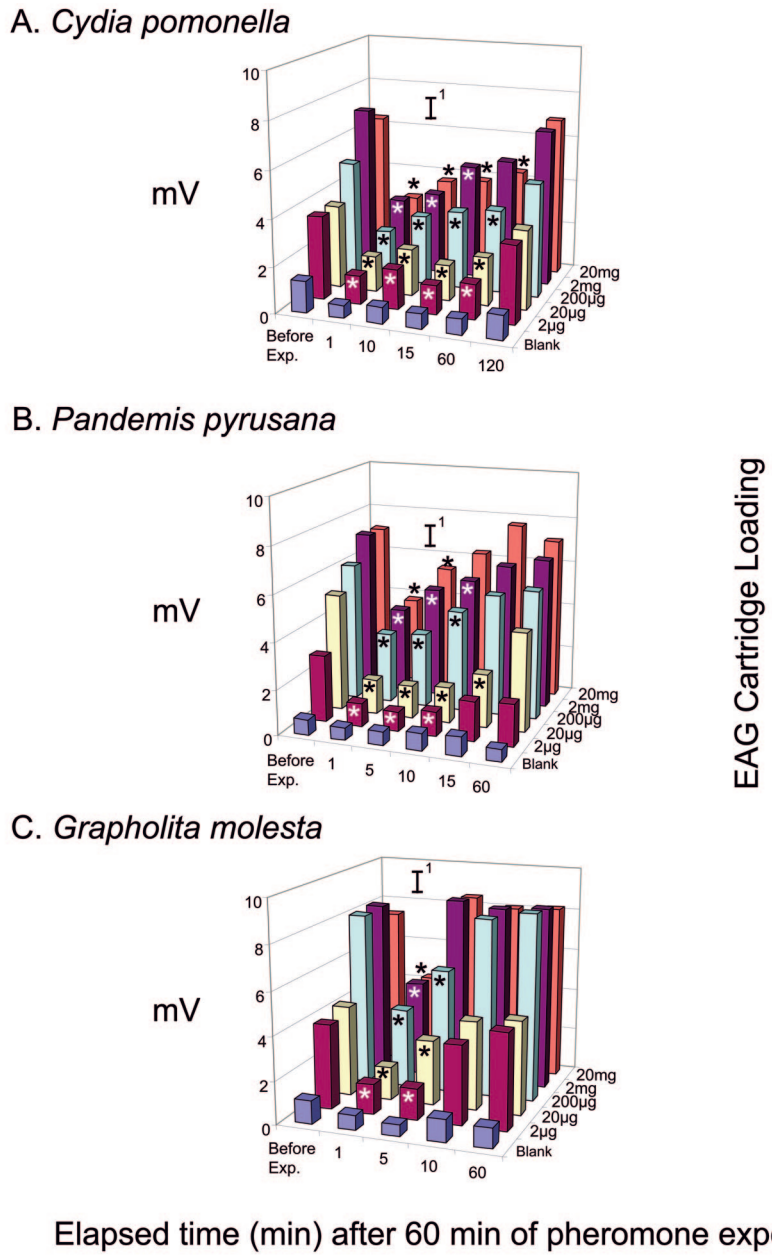

Fig. 2. Recovery from long-lasting adaptation in (A) *C. pomonella*, (B) *P. pyrusana*, and (C) *G. molesta* (n = 10–13 moths per time interval) after 60 min of confinement in adaptation chambers with the 100-mg preexposure dosage of pheromone. Bars with * indicate significant ($P < 0.05$) decrease relative to the control response. [1]Average standard error of the mean for EAG amplitude across all treatments.

Results

Effect of Pheromone Preexposure Dosage on EAG Responses. The EAG responses of male *C. pomonella* to each stimulus cartridge loading tested were significantly ($F = 11.7$; df = 7, 96; $P < 0.05$) reduced after preexposure dosages ranging from 1 to 100 mg (Fig. 1A). At the 100-μg preexposure dosage, EAG responses of *C. pomonella* were significantly ($P < 0.05$) reduced only to the 200-μg and 2- and 20-mg stimulus cartridge loadings (Fig. 1A).

The EAG responses of male *P. pyrusana* were significantly ($F = 17.1$; df = 7, 96; $P < 0.05$) reduced in response to the majority of stimulus cartridge loadings at preexposure dosages ranging from 100 μg to 100 mg (Fig. 1B). In addition, EAG responses to the 2- and 20-μg stimulus cartridge loadings were significantly

($P < 0.05$) reduced after preexposure to dosages ranging from 10 ng to 100 μg (Fig. 1B).

For male *G. molesta*, EAG responses to all stimulus cartridge loadings were significantly ($F = 9.8$; df = 7, 96; $P < 0.05$) reduced only after preexposure to the 100-mg dosage. There was a significant ($P < 0.05$) reduction of EAG response to the 2- and 20-μg stimulus cartridge loadings after preexposure to the 10-mg dosage (Fig. 1C).

Recovery from Long-Lasting Adaptation. One hour of exposure significantly ($F = 15.5$; df = 5, 60; $P < 0.05$) reduced EAG amplitudes for *C. pomonella* at most stimulus cartridge loadings for up to 60 min (Fig. 2A). By 2-h postexposure, EAG responses of *C. pomonella* were virtually indistinguishable from responses recorded before exposing moths (Fig. 2A).

EAG responses to most stimulus cartridge loadings were significantly ($F = 8.9$; df = 5, 60; $P < 0.05$) reduced for male *P. pyrusana* up to 10-min postexposure (Fig. 2B). In addition, EAG responses to the 20-μg stimulus cartridge loading were significantly ($P < 0.05$) reduced at 15-min postexposure (Fig. 2B). By 60-min postexposure, EAG responses of *P. pyrusana* were virtually indistinguishable from responses recorded before exposing moths (Fig. 2B).

For male *G. molesta*, EAG responses to all stimulus cartridge loadings were significantly ($F = 16.8$; df = 4, 48; $P < 0.05$) reduced only at 1-min postexposure (Fig. 2C). In addition, EAG responses were significantly ($P < 0.05$) reduced to stimulus cartridge loadings ranging from 2 to 200 μg at 5-min postexposure (Fig. 2C). By 10-min postexposure, EAG responses of *G. molesta* were equal to responses recorded before exposure treatment (Fig. 2C).

Discussion

LLA was documented by EAG after pheromone preexposure in two of the three species investigated. Where present, LLA was dosage-dependent and decayed over time. For *C. pomonella*, EAG responses were reduced to all of the stimulus cartridge loadings after preexposure in chambers with dosages ranging from 1 to 100 mg of (*E,E*)-8,10-dodecadien-1-ol. However, after preexposure at lower pheromone dosages (100 and 10 μg), LLA was recorded only with the higher stimulus cartridge loadings (200 μg–20 mg). Decreased EAG responsiveness was recorded up to 60 min after pheromone exposure and was completely reversed by 120 min. These results corroborate the recent findings that *C. pomonella* exposed in static chambers to 500 μg of pheromone for 10–30-min intervals also reduced EAG responsiveness for ≈1 h (Judd et al. 2005). The estimated airborne pheromone concentration that induced this decreased response (≈35 μg/liter) (Judd et al. 2005) is in the range required to induce LLA in *C. rosaceana* (Stelinski et al. 2003b).

P. pyrusana also exhibited LLA with similar characteristics to that described previously for another leafroller species, *C. rosaceana* (Stelinski et al. 2003a, b). LLA was recorded with all of the cartridge loadings after preexposure in chambers with pheromone dosages ranging from 100 μg to 100 mg. These exposure dosages correspond to airborne pheromone concentrations ranging from 19 to 56 ng of (Z)-11-tetradecenyl acetate per ml (Stelinski et al. 2003b). LLA was also recorded for *P. pyrusana* to the 2- and 200-μg cartridge loadings after preexposure dosages in chambers ranging from 10 μg to 100 ng. The 100-ng preexposure dosage yields an airborne pheromone concentration of ≈0.5 ng/ml in adaptation chambers and is the lowest concentration at which LLA is induced for *C. rosaceana* (Stelinski et al. 2003b). The LLA observed for *P. pyrusana* (Fig. 2B) was also similar to that of *C. rosaceana* in recovery time, which lasted ≈12 min (Stelinski et al. 2003a).

For *G. molesta*, reduced EAG responsiveness to all of the cartridge loadings occurred only after moths were preexposed for 1 h in chambers containing 100 mg of neat pheromone. Furthermore, recovery from adaptation was much more rapid than in the above two species. Full recovery was observed with the 2- and 20-mg stimulus cartridge loadings after 5 min and by 10 min, adaptation could no longer be detected. These results are similar to those obtained with *A. velutinana*, where LLA could not be measured by EAG 1 min after 1-h preexposures with 100 mg of neat (Z)-11-tetradecenyl acetate (Stelinski et al. 2003b). However, normal behavioral responsiveness to pheromone in both *G. molesta* (Figueredo and Baker 1992, Rumbo and Vickers 1997) and *A. velutinana* (Bartell and Roelofs 1973) is reduced for prolonged periods after pheromone exposures similar to the ones performed in our EAG studies, suggesting that habituation of the central nervous system occurs. Similar results have recently been obtained with *C. pomonella* in which behavioral responsiveness to pheromone was reduced 4 times longer than electrophysiological responsiveness (Judd et al. 2005).

There is considerable variation in the prevalence and duration of LLA among tortricid species. However, does this phenomenon have any bearing on pheromone-based mating disruption? Current data suggest that LLA is probably not an important contributing factor to mating disruption. First, the rate of recovery from adaptation in *G. molesta* and *A. velutinana*, species for which mating disruption has proven highly effective (Gut et al. 2004), is very rapid (Table 1). Stelinski et al. (2003a, b) postulated that lack of LLA may be related to higher propensity for habituation; however, this has yet to be proven. Furthermore, LLA lasts only 10–12 min in the leafrollers *C. rosaceana* and *P. pyrusana*. Only for *C. pomonella* does this effect last for upwards of 1 h. The second and more important factor suggesting that LLA is not an important contributor to mating disruption is that the physiological effect is induced at airborne concentrations of pheromone that are much higher than the 1 to 2 ng/m^3 achieved with synthetic pheromone dispensers in the field (Koch et al. 1997, 2002). However, the presence of LLA in each species does seem to be

Table 1. Prevalence of long-lasting adaptation among tortricid species versus level of difficulty for meeting requirements for successful mating disruption as defined by Gut et al. (2004)

Species	Presence (and approximate duration) of long-lasting adaptation	Level of difficulty in meeting requirements for successful mating disruption
C. rosaceana (obliquebanded leafroller)[a]	Present (12 min)	Difficult
P. pyrusana	Present (15 min)	Difficult
C. pomonella (codling moth)[b]	Present (60–75 min)	Moderate to difficult
Argyrotaenia velutinana (redbanded leafroller)[a]	Absent	Easy
Grapholita molesta (oriental fruit moth)	Absent	Easy

[a] Source data found in Stelinski et al. (2003a, b).
[b] Additional data found in Judd et al. 2005.

inversely related to their known susceptibility to mating disruption (Table 1).

It has been suggested that minutes- to hours-long exposure of male moths in the field to pheromone dispensers such as polyethylene tubes (Stelinski et al. 2003b) or repeated visits to such dispensers (Stelinski et al. 2003b, Judd et al. 2005) might cause LLA. However, Stelinski et al. (2004, 2005) found that feral *C. rosaceana*, *A. velutinana*, *G. molesta*, and *C. pomonella* approach and remain near such pheromone dispensers for very brief periods (≈30 s) in orchard plots and do not receive the required pheromone exposure to induce LLA. It is yet to be determined whether repeated visits to dispensers of synthetic pheromone induce LLA.

Peripheral adaptation occurs when olfactory receptor neurons are being directly challenged by small and large amounts of pheromone (Kuenen and Baker 1981; Baker et al. 1988, 1989), but the effect is often rapidly reversible in clean air. Reductions of behavioral responsiveness seem to last much longer than peripheral adaptation in pheromone preexposed moths, suggesting that habituation is involved (Bartell and Roelofs 1973; Figueredo and Baker 1992; Rumbo and Vickers 1997; Stelinski et al. 2003a, b; Judd et al. 2005). However, given that effective mating disruption occurs in the field at pheromone concentrations that are much lower than those required to desensitize moths by adaptation or habituation (Schmitz et al. 1997, Rumbo and Vickers 1997, Judd et al. 2005), the relevance of these mechanisms as important contributing factors to mating disruption should be questioned. Tortricid moth species are known to closely (≈0–100 cm) and briefly (≈2–30 s) approach polyethylene tube pheromone dispensers (Stelinski et al. 2004, 2005). Determining the fate of attracted moths leaving these synthetic dispensers of pheromone should help elucidate whether effects of preexposure during these visits contribute to mating disruption or whether competitive attraction between dispensers and feral females is the primary disruptive mechanism.

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