Recapture of Codling Moth (Lepidoptera: Tortricidae) Males: Influence of Lure Type and Pheromone Background

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ABSTRACT Recapture of marked male codling moths, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), released four distances from traps was measured in experiments comparing either lure type or mating disruption. Experiment 1 assessed recapture by 0.1, 1, and 10 mg of codlemone lures. Experiments 2 and 3 assessed moth recapture in orchard plots with 0, 500, or 1,000 Isomate C Plus dispensers per ha. Moths were released 1, 3, 10, and 30 m downwind of the trap in experiments 1 and 2, and 3, 10, 30, and 45 m in experiment 3. Lure type did not affect recapture, however, significantly more moths were recaptured at 3 m compared with 10 or 30 m. Most moths recaptured ≤10 m of the trap were recaptured by day 3, whereas most of the moths recaptured ≥10 m were recaptured after day 3. Thus, 0.1-, 1-, and 10-mg lures, have an attractive range of between 10 and 30 m in orchards lacking mating disruption. Both mating disruption rates greatly reduced moth recapture, and moths recaptured under a 1,000 dispenser per ha rate were recaptured from ≤10 m and within the first 2 d after release. Similar results were observed when release points were expanded to 45 m. Thus, results suggest that pheromone dispenser technologies and placement strategies that maximize disruption of males that arise within 10 m of a female are needed to markedly improve mating disruption.

KEY WORDS mating disruption, codling moth, mark–release–recapture, attractive range, spatial scale

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The codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), is the most important pest of apples (*Malus* spp.) worldwide. Codling moth is considered a quarantine pest by many nations (APHIS–PPQ 2005), making it a barrier to international trade. In the last several decades, the use of sex pheromones for mating disruption has become an important means of managing this insect with at least 160,000 ha under mating disruption worldwide (Witzgall et al. 2007).

Although mating disruption of codling moth has often been successful, there has been considerable debate regarding the behavioral mechanisms underlying how mating is disrupted (Cardé and Minks 1995, Gut et al. 2004, Miller et al. 2006). A pertinent issue for mating disruption is the quantification of the active space or attractive range of pheromone dispensers or lures, and whether the active space of lures changes in orchards under mating disruption. Knowledge about the spatial scale at which male codling moths respond to pheromone point sources of varying intensity and in varying pheromone backgrounds may provide critical information for the optimization of pheromone dispenser placement in mating disruption programs

and monitoring of codling moth populations in orchards under mating disruption.

Mark–release–recapture methodology has been used previously to show the efficacy of pheromone traps and trap competition for various Lepidoptera (Van der Kraan and Van Deventer 1982, Croft et al. 1986, Botero-Garcés and Isaacs 2004), differences in the dispersal potential of wild and laboratory-reared codling moths (Bloem et al. 1998, Knight and Light 2005, Judd et al. 2006), and differences among genetic strains of codling moth (Keil et al. 2001). Our study used mark–release–recapture for the quantification of the active space or attractive range of three codlemone lures: 0.1, 1, and 10 mg in an orchard lacking a pheromone background as well as the attractive range of the 0.1-mg lure in orchard blocks lacking mating disruption or with half or full labeled rates of pheromone dispensers. Our hypotheses were that a greater proportion of moths would be recaptured from release sites closer to the traps; that recapture from 30 m would be higher for higher load lures and that mating disruption would reduce the distance from which moths were recaptured.

Materials and Methods

Study Site and Plot Layout. The experiments were carried out in a commercial apple orchard near Quincy, WA (47° 14′01″ N, 119° 51′08″ W) planted with dwarfing rootstock grafted to 'Fuji' apples with a

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row spacing of 4.6 m and a planting density of 2,250 trees per ha. Orchard rows were oriented north–south and trees were between 4 and 5 yr old and were between 2.7 and 3 m in height. Prevailing winds came from the northwest of the orchard. The experimental orchard consisted of two orchard blocks measuring ≈377 m east to west and 366 m north to south, which were further subdivided into two half blocks separated by a drive row. The northern half of the northern block and both halves of the southern block were selected for the study.

The three orchard subblocks were each divided into three experimental units consisting of 14 rows (64 m in width) with a delta style pheromone trap (LPD Scenturion Guard-post, Suterra, Bend, OR) hung at the approximate center of each experimental unit at 2.5 m in height and ≈30 m from the northern edge of the block. A buffer of 17 rows (77 m) was maintained between each experimental unit and a buffer of three rows (14 m) was maintained from orchard edges. The resulting nine experimental units were arranged in three blocks with trees oriented north–south, three experimental units within each block.

Insects. Codling moths were obtained from the USDA–ARS Yakima Agricultural Research Laboratory (YARL) colony. Two thirds of the moths used in the experiments were internally marked through the addition of Calico red oil to their diet (Charmillot 1979). Moths were received as pupae and sorted by sex, after which they were allowed to emerge at room temperature. Adult moths were collected daily and stored in a temperature cabinet set at 4.5°C. The photoperiod for both the emergence room as well as the temperature cabinet was synchronized with the ambient photoperiod with weekly adjustments. All moths released in the experiments were <48 h old. Cooled moths were marked using four colors of fluorescent powder (BioQuip, Rancho Dominguez, CA) by placing them in a petri dish coated with 20 mg of powder and gently agitating the dish. After marking, moths were placed in a release cup consisting of two overlapping 90-ml S-300 portion cups (Prairie Packaging, Bedford Park, IL), with five 4-cm-diameter holes punched in the inner cup. During transport, and before their release, moths were kept in a cooler. Moths were released between 10 a.m. and 12 p.m. by hanging the release device on an orchard trellis wire ≈1.5 m in height and gently removing the outer cup from the cup with holes in it. Releases were performed each Monday, and traps were checked daily Monday through Friday. Internal markings were used to differentiate between releases (i.e., marked/unmarked moths were alternated among the three blocks).

A trial comparing the recapture of male codling moths marked with the four fluorescent powders as well as unmarked moths was conducted between 24 August and 28 September 2007 at the Washington State University Tree Fruit Research and Extension Center campus in Wenatchee, WA. Ten internally marked moths for each powder color were released 5 m from a trap baited with a 0.1-mg codlemone lure. The experiment was conducted in four experimental blocks and replicated five times. An analysis of variance with powder color nested within block was used to analyze recapture rate.

Experiment 1. Experiment 1 compared recapture of male codling moth released at four distances from a single pheromone trap baited with a 0.1-mg codlemone lure (98% isomeric and chemical purity; Suterra, Bend, OR), an L2 monitoring lure (1 mg of codlemone; Trécé Inc., Adair, OK), or a BioLure (10 mg of codlemone; Suterra). The experiment was conducted between 29 May and 7 July 2006 with four experimental runs. Ten codling moth males were released 1, 3, 10, and 30 m downwind of each trap with a different mark used at each distance. Lures were preaged by placing them in a laboratory fume hood at room temperature for 12 h before deployment in the field; lures were replaced weekly. Lures were arrayed in a 3 by 3 Latin Square design with lure types rotated through the experimental units weekly and fresh lures used for each experimental run. Thus, each experimental run consisted of three replicates for a total of 12 replicates over the four runs.

Experiment 2. Experiment 2 was conducted between 10 July and 31 July 2006. In this experiment, background pheromone release rate was manipulated with lure type constrained to a 0.1-mg lure. The 0.1 mg lure was selected for this trial based on a previous study that indicated that it was the best female mimic compared with several other commercially available lures and dispensers (J.F.B. and M. Doerr, unpublished data). Three treatments were examined including zero, half (500 dispensers per ha), and full (1000 dispensers per ha) labeled rates of Isomate C Plus (Shin-Etsu Chemical Co., Tokyo, Japan). Dispensers contained 205 mg of 53.0% codlemone [(E,E)-8,10-dodecadien-1-ol], 29.7% 12:OH, 6.0% 14:OH, and 11.3% inert ingredients. Pheromone dispensers were applied on 3–4 July at ≈2.25 m in height in the tree canopy. Pheromone was applied in the 14 rows making up each experimental unit. The arrangement left a buffer of 17 untreated rows (73.6 m) between experimental units. Due to the nature of the pheromone treatments, randomization and rotation of treatments were not possible for this experiment. Instead, the three rates of pheromone background were arrayed in such a way to minimize interference with the zero rate in the western (most upwind) experimental units, the half rate in the central experimental units, and the full rate at the eastern experimental units (most downwind). Ten marked codling moth males were released 1, 3, 10, and 30 m downwind of each trap. Each of the three experimental runs consisted of three replicates for a total of nine replicates.

Experiment 3. Experiment 3 was conducted in four trials between 1 and 28 August 2006 and was similar to experiment 2, with the exception that release distances from the trap were 3, 10, 30, and 45 m. Each experimental run consisted of three replicates for a total of 12 replicates over the four runs.

Data Analysis. Experiments were analyzed using two generalized linear mixed models. The first model evaluated the total number (cumulative) of marked

codling moths recaptured at each experimental unit at the end of the week-long observation period, whereas the second model assessed daily recapture of moths using a repeated measures approach.

Total Weekly Recapture. The total number (cumulative) of codling moths recaptured in each experimental plot throughout each release period was modeled using a generalized linear mixed model fitted with the GLIMMIX procedure of SAS (SAS Institute 2004). In all three experiments, the response variable was best fit using a negative binomial distribution. In experiment 1 (lure dosage), the statistical model included the fixed effects of lure type and release distance in a split-plot arrangement that recognized lure type as the main plot factor and distance as the split-plot factor, each with corresponding sizes of experimental units. The model also included blocks along both the northern and eastern axes of the study orchard, as well as experimental run, as random blocking factors. In experiments 2 and 3 (mating disruption rate), total weekly recapture was analyzed using a split-plot arrangement of fixed effect factors in a randomized complete block design with block and experimental run designated as random effects, mating disruption rate as the main plot factor (three levels) and distance from trap as the subplot factor (four levels). For all three experiments, least square means were estimated and post hoc pairwise comparisons were conducted using Tukey–Kramer adjustment to avoid inflation of type I error rate.

Daily Recapture. We analyzed the temporal pattern of recapture for each of the experiments using a generalized linear mixed model fitted with the GLIMMIX procedure (SAS Institute 2004). The response variable was the number of daily recaptured moths and was modeled using a binomial distribution that considered the remaining unrecaptured moths on a given day as the total number of possible recapture events. Due to an extreme category problem (quasi-complete separation of data points), the response variable was redefined as the sum of daily recaptured moths across spatial replicates (blocks). In addition, a separate statistical model was fitted to each release distance within each experiment, to allow for model convergence (i.e., four models for each experiment). The statistical model included the fixed effects of lure type or mating disruption (experiment 1 or experiments 2 and 3, respectively), day and their two-way interaction, as well as the random effect of run within treatment to appropriately recognize experimental units and account for the repeated measures design. For experiments 2 and 3, the interaction between day and treatment were excluded from the model due to model overparameterization leading to unstable variance structure and inflated *P* values. Furthermore, daily moth survival as predicted using a degree-day model created and validated by Jones and Wiman (2008) was fitted as an adjusting covariate in the model to account for the natural, temperature dependent mortality of moths over the course of the experiment. An overdispersion parameter was fit when appropriate and an adaptive Gauss-Hermite quadrature method was used to approximate the marginal log likelihood and expedite
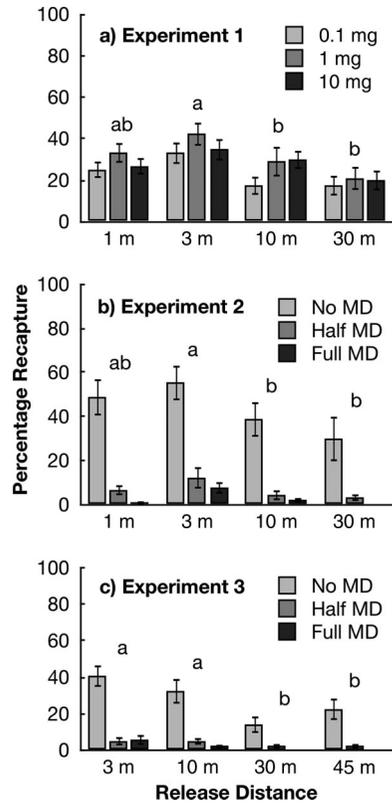

Fig. 1. Cumulative average percentage ($\pm$ standard error of the mean) recapture of male codling moth for Experiment 1 (a), 2 (b) and 3 (c) by distance and lure. Experiment 1 was conducted in the absence of mating disruption while experiment 2 and 3 were conducted with 0.1 mg codlemone lures. Significant differences among release distances are indicated with different letters (Tukey-Kramer adjusted pair wise comparisons $p < 0.05$).

model convergence for the 1- and 30-m release distances in experiments 1 and for all release distances for experiments 2 and 3. Least square means were estimated and post hoc pairwise comparisons were performed using a Tukey–Kramer adjustment to avoid inflation of type I error rate.

Results

Experiment Testing Potential Impact of Marking on Recapture. No significant differences were detected in the recapture of moths based on powder presence or color ($F = 0.47$; df $= 5, 108$; $P = 0.80$).

Experiment 1. Release distance from the trap significantly affected the total number of recaptures ($F = 6.44$; df $= 3, 131$; $P < 0.001$) (Fig. 1a), such that recapture was greater at the 3-m release distance compared with 10- and 30-m distances. Recapture of moths released 1 m from the trap was intermediate and not significantly different from either release distance groups. Lure type was a nearly significant factor for total recaptures ($F = 2.68$; df $= 2, 131$; $P = 0.072$). The proportion of total weekly recaptures was 28, 37, 26,

Table 1. Mean ± SE of recaptured marked moths within release distances, lure type, and day combinations in experiment 1

Day	1-m release distance			3-m release distance		
	0.1 mg	1 mg	10 mg	0.1 mg	1 mg	10 mg
1	5.00 ± 2.80aA	6.00 ± 1.29aA	5.25 ± 1.80aA	5.25 ± 2.39aA	5.00 ± 2.36aA	4.00 ± 2.48aA
2	1.50 ± 0.96aAB	3.00 ± 1.47aA	1.75 ± 1.44aAB	2.25 ± 1.65aA	4.00 ± 3.08aA	3.50 ± 1.55aA
3	0.50 ± 0.50aB	0.25 ± 0.25aB	0.25 ± 0.25aAB	1.75 ± 1.11aA	2.50 ± 1.55aA	1.50 ± 1.19aA
4	0.00 ± 0.00abAB	0.00 ± 0.00bC	0.50 ± 0.50aB	0.25 ± 0.25aA	0.50 ± 0.50aA	0.50 ± 0.50aA
	10-m release distance			30-m release distance		
1	2.00 ± 1.68aA	4.00 ± 3.03aA	4.50 ± 3.30aA	1.00 ± 2.80aB	1.75 ± 1.75aB	2.00 ± 2.00aB
2	1.00 ± 1.00aA	2.00 ± 1.35aA	1.50 ± 1.19aA	0.25 ± 0.96aAB	0.50 ± 0.50aAB	0.00 ± 0.00aAB
3	2.00 ± 2.00aA	1.25 ± 1.25aA	2.25 ± 1.93aA	2.75 ± 0.50aA	2.50 ± 2.18aA	2.25 ± 2.25aA
4	0.25 ± 0.25aA	0.25 ± 0.25aA	0.25 ± 0.25aA	0.50 ± 0.00aAB	0.25 ± 0.25aAB	0.25 ± 0.25aAB

Means within a release distance followed by different lowercase and uppercase letters are significantly different among lure type (row), and day of recapture (column), respectively ($\alpha = 0.05$; Tukey-Kramer adjusted pairwise comparisons).

and 19% of moths for codling moth males released at the 1-, 3-, 10-, and 30-m distances, respectively (Fig. 1a).

In the repeated measures analysis of moth recapture for moths released at 1 m, a significant interaction between lure type and day was identified on the number of moths recaptured ($F = 32.78$; df = 5, 26; $P < 0.001$). Table 1 presents a summary of factor combinations that differed significantly. In general, all three lures recaptured more moths on day 1 than on days 3 or 4. No significant factors were detected for moths released at 3 or 10 m; however, a significant day effect was found for moths released at 30 m ($F = 5.31$; df = 3, 26; $P = 0.006$); moths were more frequently recaptured on day 3 compared with day 1 ($t = -2.79$, df = 26, $P = 0.0448$). Note that, in some cases, model conclusions may not be intuitive because the statistical model accounted for the number of moths recaptured on previous days as well as predicted natural mortality, which are not apparent in raw averages shown in the tables and figures. Thus, moths recaptured at later dates may have had a larger effect on the model than moths recaptured earlier.

Experiment 2. As expected, mating disruption had a highly significant effect on the total number of weekly recaptures, with far fewer moths recaptured under half or full rates versus the control (no dispensers) ($F = 25.83$; df = 2, 4; $P = 0.005$). The rate of mating disruption (i.e., half versus full rate) did not seem to

have a significant impact on recapture; however, the numerical trend was for a greater proportion of moths to be recaptured in the half rate compared with the full rate. Distance had a significant effect on the total number of weekly recaptures ($F = 5.14$; df = 3, 96; $P = 0.002$). For the blocks lacking mating disruption, an average of 49, 56, 39, and 30% of moths per run were recaptured from 1, 3, 10, and 30 m, respectively. For the half rate of mating disruption, 7, 12, 4, and 3% of moths per run were recaptured from 1, 3, 10, and 30 m, respectively. For the full rate of mating disruption, a meager 1, 8, 2, and 0% of moths per week were recaptured from 1, 3, 10, and 30 m, respectively. Least squares means comparisons performed on the distance main effect indicated significantly more total moths recaptured at 3 m release distance compared with 10- and 30-m distances (Fig. 1b).

In the repeated measures analysis for experiment 2, significant effects of mating disruption rate were detected for 1-, 3-, 10-, and 30-m release distances ($F = 9.51$; df = 2, 6; $P = 0.014$, $F = 13.87$; df = 2, 6; P 0.006, $F = 15.93$; df = 2, 6; $P = 0.004$, and $F = 14.26$; df = 2, 6; $P = 0.009$, respectively) as well as for recapture days 1, 2, 3, and 4 ($F = 3.45$; df = 3, 23; $P = 0.033$, $F = 13.87$; df = 2, 6; P 0.006; $F = 15.93$; df = 2, 6; $P = 0.004$ and $F = 14.26$; df = 2, 6; $P = 0.009$, respectively). Specific differences between levels of main effects are presented in Table 2. Model conclusions were not always

Table 2. Mean ± SE of recaptured marked moths within release distances, level of mating disruption, and day of recapture in experiment 2

Day	1-m release distance			3-m release distance		
	No MD	Half rate MD	Full rate MD	No MD	Half rate MD	Full rate MD
1	8.33 ± 2.80aA	1.33 ± 0.67bA	0.00 ± 0.00bA	8.33 ± 3.38aA	2.67 ± 1.67bA	1.67 ± 0.67bA
2	3.00 ± 0.96aB	0.67 ± 0.33bB	0.33 ± 0.33bB	2.67 ± 2.19aB	1.00 ± 1.00bB	0.33 ± 0.33bB
3	1.33 ± 0.50aB	0.00 ± 0.00bB	0.00 ± 0.00bB	2.33 ± 2.33aB	0.00 ± 0.00bB	0.33 ± 0.33bB
4	1.33 ± 0.00aAB	0.00 ± 0.00bAB	0.00 ± 0.00bAB	1.33 ± 0.88aC	0.00 ± 0.00bC	0.00 ± 0.00bC
	10-m release distance			30-m release distance		
1	3.33 ± 2.40aA	0.33 ± 0.33bA	0.33 ± 0.33bA	0.00 ± 0.00aA	0.33 ± 0.33bA	0.00 ± 0.00cA
2	1.67 ± 0.88aC	0.33 ± 0.33bC	0.33 ± 0.33bC	1.67 ± 0.67aA	0.33 ± 0.33bA	0.00 ± 0.00cA
3	3.33 ± 2.85aB	0.00 ± 0.00bB	0.00 ± 0.00bB	4.33 ± 2.33aA	0.00 ± 0.00bA	0.00 ± 0.00cA
4	1.67 ± 1.67aD	0.33 ± 0.33bD	0.00 ± 0.00bD	2.33 ± 1.86aB	0.00 ± 0.00bB	0.00 ± 0.00cB

Means within a release distance followed by different lowercase and uppercase letters are significantly different among mating disruption (MD), rate (row), and day of recapture (column), respectively ($\alpha = 0.05$; Tukey–Kramer adjusted pairwise comparisons). Only main effect differences are shown as inclusion of the interaction effect caused overparameterization.

Table 3. Mean ± SE of recaptured marked moths within release distances, level of mating disruption and day of recapture in experiment 3

Day	3-m release distance			10-m release distance		
	No MD	Half rate MD	Full rate MD	No MD	Half rate MD	Full rate MD
1	10.50 ± 2.99aA	0.75 ± 0.48aB	1.75 ± 0.75aB	10.50 ± 3.12aA	0.50 ± 0.29aB	0.50 ± 0.29aB
2	0.00 ± 0.00aA	0.00 ± 0.00aB	0.00 ± 0.00aB	0.00 ± 0.00aA	0.25 ± 0.25aB	0.00 ± 0.00aB
3	0.25 ± 0.25aA	0.50 ± 0.50aB	0.00 ± 0.00aB	0.25 ± 0.71aA	0.50 ± 0.50aB	0.00 ± 0.00aB
4	0.25 ± 0.25aA	0.00 ± 0.00aB	0.00 ± 0.00aB	0.25 ± 0.00aA	0.00 ± 0.00aB	0.00 ± 0.00aB
	30-m release distance			45-m release distance		
1	1.75 ± 1.44aA	0.25 ± 0.25aA	0.00 ± 0.00aA	3.25 ± 2.93aAB	0.00 ± 0.33aAB	0.00 ± 0.00aAB
2	0.00 ± 0.00aA	0.25 ± 0.25aA	0.00 ± 0.00aA	0.00 ± 0.00aB	0.25 ± 0.33aB	0.00 ± 0.25aB
3	0.50 ± 0.50aA	0.00 ± 0.00aA	0.00 ± 0.00aA	1.00 ± 0.58aA	0.25 ± 0.00aA	0.00 ± 0.25aA
4	0.50 ± 0.50aA	0.00 ± 0.00aA	0.00 ± 0.00aA	0.75 ± 0.75aAB	0.25 ± 0.00aAB	0.00 ± 0.25aAB

Means within a release distance followed by different lowercase and uppercase letters are significantly different among mating disruption (MD) rate (row), and day of recapture (column), respectively ($\alpha = 0.05$; Tukey–Kramer adjusted pairwise comparisons). Only main effect differences are shown as inclusion of the interaction effect caused overparameterization.

intuitive because the model accounted for the number of moths recaptured on previous days as well as predicted natural mortality. Furthermore, treatment interactions were not assessed as their inclusion caused overparameterization. Plots with full and half rates of mating disruption recaptured significantly fewer moths compared the plots without disruption for all four distances. However, varying differences were detected for daily recapture depending on release distance. Significantly more moths released at 1 m were recaptured on day one versus days 2, 3, and 4. Significantly more moths released at 3 m were recaptured on day one versus the remaining days and on days 2 and 3 compared with day 4. The number of moths recaptured differed significantly among all days for moths released at 10 m with recaptures on day 1 > day 2 > day 3 > day 4. Significantly more moths released at 30 m were recaptured on day four versus days 1, 2, and 3.

Experiment 3. As in experiment 2, mating disruption rate and moth release distance were both found to be significant determinants of moth recapture ($F = 67.75$; df = 2, 4; $P < 0.001$ and $F = 5.51$; df = 3, 240; $P = 0.001$, respectively). Again, fewer moths were recaptured under half or full rates versus the control (no dispensers). Pairwise comparisons indicated a consistent pattern among distances for the three pheromone lures, with significantly more moths recaptured at the three and 10-m distances compared with the 30- and 45-m distances (Fig. 1c). In blocks lacking mating disruption, 41, 33, 15, and 23% of moths per run were recaptured from 3, 10, 30, and 45 m, respectively. For the half rate of mating disruption, 5, 5, 3, and 3% of moths per run were recaptured from 3, 10, 30, and 45 m, respectively. For the full rate of mating disruption, 6, 3, 0, and 0% of moths were recaptured from 3, 10, 30, and 45 m.

Repeated measures analysis for experiment 3 yielded surprisingly different results than experiment 2. Significant effects of mating disruption rate were detected for the 3- and 10-m distances ($F = 8.25$; df = 2, 9; $P = 0.009$ and $F = 6.58$; df = 2, 9; $P = 0.017$, respectively) but not the 30- and 45-m distances ($F = 2.4$; df = 2, 9; $P = 0.15$ and $F = 1.27$; df = 2, 9; $P = 0.328$,

respectively). Significant effect of day of recapture was detected for 10- and 45-m release distances ($F = 3.1$; df = 3, 32; $P = 0.041$ and $F = 3.35$; df = 3, 32; $P = 0.031$, respectively) but not the 3- or 30-m release distances ($F = 0.41$; df = 2, 32; $P = 0.7467$ and $F = 1.05$; df = 3, 32; $P = 0.384$, respectively). Specific differences between levels of main effects are presented in Table 3. Once again, model conclusions are not necessarily intuitive because the model accounted for the number of moths recaptured on previous days as well as predicted natural mortality and factor interactions were omitted due to model overparameterization. The 3- and 10-m release rates plots with full and half rates of mating disruption recaptured significantly fewer moths compared with the plots without disruption. Although day was a significant factor for moths released at 10 m, none of the pairwise comparisons reached statistical significance. However, significantly more moths were recaptured for the 45-m release distance on day 3 compared with day 4.

Discussion

Quantifying active space or attractive range of pheromone lures is challenging because the "active space" results from dynamic interactions arising from the target insect's physiology as well as its abiotic environment. Ambient temperature and wind velocity and consistency are examples of abiotic factors that influence this phenomenon. Bloem et al. (2006) found that rates of movement of both male and female codling moth in the laboratory increased as temperatures increased to 25°C. Our own laboratory and field studies of codling moth flight behavior at varying wind speeds indicate that the majority of orientation to synthetic pheromones occurs at speeds under 0.3 m/s (M.J.G. and V.P.J., unpublished data). Furthermore, Van der Kraan and Van Deventer (1982) reported that the speed and consistency of wind had a marked impact on the active space of pheromone traps for the tortrix *Adoxophyes orana* (F.v.R.) (Lepidoptera: Tortricidae). Likewise, Bacca et al. (2006) found that wind direction and intensity moderated the amount of trap interference detected in a coffee (*Coffea* spp.) leaf-

miner, *Leucoptera coffeella* (Guein-Meneville) (Lepidoptera: Lyonetidae) monitoring study.

An additional challenge for studies of pheromone attractive range is the determination of what constitutes a realistic response for the study animal. To illustrate; a study performed by Mankin et al. (1999) used acoustic signals generated by the wing beat frequency of the Indianmeal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae), in addition to observations of caged male moths to assess response to a pheromone trap. Although interpretation of trap active space using behaviors such as these has definite merit, in the context of mating disruption, activation of orientation behavior is not a complete predictor of whether a male moth will contact a target pheromone source due to the large amounts of pheromone present and potential for overlapping pheromone plumes. Thus, moth captures in pheromone traps may provide a more complete measure of the spatial scale and success rate at which codling moth can locate pheromone sources.

Despite these challenges our data demonstrate consistent variations of recapture in response to release distance, time, and pheromone background. In both experiments 1 and 2, moths released at 3 m provided the numerical peak of recapture when released in the absence of mating disruption, with significantly more moths recaptured at 3 m than at 10 or 30 m (Fig. 1a and b). That slightly fewer moths were recaptured at 1 m compared with 10 m is perhaps not surprising because moths released so close to the trap could have flown upwind of or away from the trap during their initial dispersal; and, once sufficiently far from the trap's plume, they may have been less likely to locate it. If we consider the aggregate pheromone plume released by a given lure to be roughly cone shaped, simple angular effects might explain this, with the likelihood of the moth being in the cone of the plume increase by the square of the distance. In this case, the angle of the cone (φ) is a function of wind speed and consistency with the area of the cone defined by $\tan(\Phi) \times \Pi \times$ distance^2. Thus, moths beginning their flight at 1 m from the trap may have a smaller chance of encountering the pheromone plume (where the "cone" is narrow) versus moths released further downwind (where the "cone" is wider). This line of reasoning suggests a minimum attractive range as well as a maximum one. Whether this phenomenon would apply to males responding to females is debatable, because visual cues have been shown to be important in the range of <1 m (Castrovillo and Cardé, 1980).

Lure type did not affect overall percentage recapture at any of the release distances tested, although the 1-mg lure caught numerically more moths at all but the 10-m release distance (Fig. 1a). There were significant differences in the temporal pattern of recapture by lure type, but the direction of this difference seems to be affected by the day of recapture, with the 1-mg lure performing numerically better than the other two lures during the first 3 d and the 10-mg lure performing significantly better than the 1 mg and marginally better than the 0.1-mg lure on day 4. These results suggest that the peak attractive range of the two lower dose lures is probably between 3 and 10 m but may be somewhat larger for the 10-mg lure. This conclusion is within the range of results found for pheromone traps for a coffee leafminer (Bacca et al. 2006), grape berry moth, *Endopiza viteana* Clemens (Lepidoptera: Tortricidae) (Botero-Garcés and Isaacs 2004), and the tortrix *A. orana* (Van der Kraan and Van Deventer 1982).

Moth recapture by day for the experiment 1 and to a lesser extent for experiment 2 suggest that many of the moths released at 30 m may have taken three successive nights to come into the attractive range of the traps. This is most visible in a shift in the pattern of recapture for experiment 1 within the four distances, with lure specific effects visible for the 1-m release and more moths recaptured on the first day versus the third and fourth, a lack of significant differences for the 3- and 10-m release distances and then a significantly higher proportion of moths recaptured on the second and third day versus the first at 30 m (Table 1). This further supports the hypothesis that attractive range of the lures tested is in the neighborhood of 10 m in the absence of mating disruption.

The pattern of recapture in our second and third experiments indicates that mating disruption using hanging pheromone dispensers has a marked impact on recapture of codling moth from all distances tested and that this effect may increase with dispenser density. Although we did not detect a significant difference between the half and full rate of mating disruption the full rate was numerically lower than the half rate at each release distance and eliminated recapture at the further distances. This was apparent in both total percentages recaptured (Fig. 1b and c), as well as in temporal pattern of recapture (Tables 2 and 3, respectively). However, the pattern of recapture among the distances tested seemed to be similar among treatments, indicating that mating disruption may have a relatively constant reducing effect on the moths' ability to find the trap. This could be construed to support the recent hypothesis of Miller et al. (2006) that point source competition is likely the primary mode of disruption provided by hanging dispensers.

A study by Epstein et al. (2006) indicated a similar pattern, with higher levels of mating disruption observed as pheromone dispenser density increased. The significant reduction of trap attractive range from 45 versus 10 m under a full rate of mating disruption (1,000 Isomate C Plus per ha) has significant consequences for this important pest, namely, that emigrating male moths may be of less consequence to codling moth pest management than males emerging in the proximity of females (Duthie et al. 2003). Thus, the data presented reinforce the importance of maintaining low local populations of codling moth for maximizing the effect of mating disruption (Cardé and Minks 1995, Gut et al. 2004).

Daily patterns of recapture under mating disruption also provide interesting information regarding how mating disruption may function over time. In the second experiment, moths in plots with mating disruption

were almost always recaptured within the first 2 d after release. In contrast, in plots lacking mating disruption, moths were recaptured fairly consistently 3 and 4 d after release (Table 2). One interpretation of this pattern is that moths within the disrupted plots not recaptured within the first 2 d were drawn away from the trap by competing dispensers and were unlikely to return to the area of the trap (Epstein et al. 2006). Alternatively, it also might be possible that moths not recaptured quickly became habituated or desensitized to pheromone (Stelinski et al. 2006) making them unable to locate the trap. However, a study completed by Judd et al. (2005) supports the hypothesis that for habituation and desensitization of codling moth to take place in the field, males must orient to within a short distance of pheromone dispensers. This suggests that mating disruption in this species may arise from a combination of these two modes of action in concert. In either case, a delay in mate finding may have severe consequences because male moth longevity may be as short as 3 d (Jones and Wiman 2008) and delayed mating has severe impacts on both sperm viability as well as female fertility (Jones et al. 2008). Thus, by delaying mating events by even 1 or 2 d, mating disruption may have a marked impact on codling moth populations.

Inconsistencies among the temporal pattern of recapture among experiments 1, 2, and 3 in the plots lacking mating disruption are also of interest. Moths in experiment 3 were typically all recaptured on day one, regardless of the release distance (Table 3), whereas moths were recaptured throughout the week in experiments 1 and 2. One potential explanation for this phenomenon is variation in degree-day accumulations during the first day after release among the three experiments. The overall trend was one of increasing degree-day accumulation with 11.03, 14.10, and 16.50 average degree-days accumulated on the first day of the three experiments, respectively. Hotter ambient conditions in the latter two experiments also may have contributed to the increase in total moths recaptured compared with the experiment 1 (Fig. 1). The hypothesis that moths may have moved farther under increased temperature conditions is supported by a study by Bloem et al. (2006) that reported increased codling moth activity on flight mills at temperatures >25°C. Thus, future studies should consider the impact of ambient temperature on the mate foraging behavior of codling moth and its impact on mating disruption. Likewise data collected in Wenatchee, WA, suggest that wind speed may have a serious impact on codling moth's ability to orient to sex pheromones (M.J.G. and V.P.J., unpublished data).

The quantification of different spatial scales at which mating disruption takes place, and whether dispenser density versus dispenser release rate may be more important for finer or broader spatial scales are two important questions for the improvement of mating disruption. Our data suggests that disruption of codling moth with Isomate C Plus dispensers is most effective at distances >3 m, and work by Duthie et al. (2003) indicates that this species can locally aggregate

as larvae. Thus, two specific behavioral questions that need to be addressed are the impact of exposure to synthetic pheromone plumes on male response to nearby females as well as whether such exposure changes the rate at which males leave pupal aggregations after eclosion.

In conclusion, our data prove that deployment of Isomate C Plus dispensers at either a half- or full-labeled rate significantly reduces the spatial scale at which moth orientation to a trap are successful (Fig. 1b and c). Based on previous findings that increased densities of codling moth likely leads to increased larval aggregations (Duthie et al. 2003) and random encounters of adult codling moth males and females in the canopy are probably positively correlated to increased population density (Barclay and Judd 1995), our data provide a spatial scale based explanation for reported failures of mating disruption in orchards with high densities of codling moth (Cardé and Minks 1995, Gut et al. 2004). Important questions for future studies are whether the addition of more dispensers can provide better disruption for moths orienting from within 10 m and whether there is a minimum dispenser dosage required to provide mating disruption.

Acknowledgments

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