

Edge Effects in the Directionally Biased Distribution of *Choristoneura rosaceana* (Lepidoptera: Tortricidae) in Apple Orchards

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ABSTRACT Edge effect tests have been used in a number of studies on obliquebanded leafroller, *Choristoneura rosaceana* (Harris), to test for evidence of mated female immigration into pheromone-treated orchards. This type of test compares obliquebanded leafroller presence or activity around the perimeter of an orchard against presence or activity in the interior. Higher numbers detected around the edges of an orchard would indicate higher levels of flight activity at the edge, a pattern that could be generated by high levels of immigration. Recent work has shown that the spatial distribution of recaptured obliquebanded leafroller adults released from a single location can be directionally biased, which could obscure the ability to detect an edge effect. To test this theory, data from an orchard study conducted in 1991 that found no significant edge effect was reanalyzed. When we accounted for the directional bias in the distribution of first-generation mated female moths, we found an edge effect with significantly more mated females captured in the edge traps than in the center or mid-interior traps. No edge effect was found when the directional bias was ignored. In addition, second-generation males and mated females both showed a significant edge effect that had not been detected in the original analysis, which had combined both first- and second-generation data.

KEY WORDS directional orientation, immigration, dispersal, edge effects, pheromone control

Obliquebanded leafroller, *Choristoneura rosaceana* (Harris), is a key pest in apples (Reissig 1978, Madsen et al. 1984, Agnello et al. 1996, Lawson et al. 1996, Pree et al. 2001), pears (Knight et al. 1998, Pree et al. 2001), cherries (Knight et al. 1998), filberts (AliNiazee 1986), raspberries (Li et al. 1995, Li and Fitzpatrick 1997), and peaches (Pree and Roberts 1981, Kaethler et al. 1982). Attempts to control obliquebanded leafroller in apple orchards using pheromones for mating disruption have shown inconsistent results (Agnello et al. 1996, Lawson et al. 1996, Knight et al. 1998, Trimble and Appleby 2004, Stelinski et al. 2005), and damage in pheromone-treated orchards can be above acceptable levels (Agnello et al. 1996). One possible explanation for these results is mated female immigration. The immigration behavior of mated females is considered the “most crucial trait” affecting the susceptibility of a pest to control using pheromone disruption (Cardé and Minks 1995). If there is substantial immigration of gravid females into a pheromone-treated orchard, even complete disruption of within-orchard mating might not result in sufficient suppression of pest damage.

One common method used to detect immigration is an edge effect test that compares insect presence or activity around the perimeter of a site with that in the interior. Higher numbers detected around the edges

of an orchard would indicate higher levels of flight activity at the edge, a pattern that could be generated by high levels of immigration.

In previous studies testing for an edge effect in obliquebanded leafroller distributions, no differences were found in the percentage of male, mated female, or virgin female adults captured in traps located at the edge or interior of orchards (Agnello et al. 1996, Lawson et al. 1996, Knight et al. 1998). Studies have looked for differences in the number of moths captured using molasses bait traps (Agnello et al. 1996), differences using passive interception traps (Lawson et al. 1996), and differences in the number of tethered virgin females that were mated in edge and interior traps (Lawson et al. 1996, Knight et al. 1998). Measures of larval infestation and fruit damage also showed no differences between edge and interior locations (Lawson et al. 1996, Knight et al. 1998).

The absence of an edge effect in orchards has been attributed to the possibility that most obliquebanded leafrollers originate within the apple orchard or that immigrating moths cannot be detected using the trapping methods available (Lawson et al. 1996). We suggest another possible reason is directionally biased immigration, which would result in some edge traps having consistently higher catches than others. Mark-release-recapture experiments done by Hsu (2002) found a significant directional bias in the spatial distribution of recaptured male, mated female, and virgin

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female obliquebanded leafroller adults released from a single location in an experimental apple orchard that had no artificial pheromone treatments. Directionally biased immigration could make it more difficult to detect a statistically significant difference between the edge and interior treatments because the edge traps would have a higher variance because of the biased spatial distribution of the moths.

To test this possibility, we reanalyzed data from a 1991 study (Agnello et al. 1996) conducted in pheromone-treated orchards to determine whether a directional bias in the spatial distribution of moths could interfere with the ability to detect a statistically significant edge effect.

Materials and Methods

Agnello et al. (1996) conducted a series of pheromone control studies in grower orchards between 1989 and 1992. We reanalyzed data from their 1991 study. The 1991 study used four orchards (hereafter referred to as orchards 1, 2, 3, and 4) in Orleans and Wayne Counties, NY. Each orchard contained two types of pheromone dispensers releasing an obliquebanded leafroller natural pheromone blend (90:5:5% Z/E11-14:OAc, Z11-14:OH). In each orchard, 24 bait traps were arranged in concentric rings at three locations: 4 traps in the center, 8 traps in the mid-interior, and 12 traps placed around the edge (Agnello et al. 1996). The bait traps consisted of a 1-liter plastic bucket covered with hardware cloth (0.6-cm² mesh) and baited with 300 ml of molasses and granulated baker's yeast bait (1:10 molasses:water plus 1.1 g of yeast per liter of solution). Bait traps were hung from scaffold branches ≈1 m above ground.

Moths were collected 21 times over the season, twice weekly between 22 May and 27 August 1991. In general, the first-generation flight of obliquebanded leafroller moths begins in early June and the second-generation flight begins in early August. In 1991, first-generation moths were captured on the first trapping date, 22 May, and the second-generation flight started in mid-July (Agnello et al. 1996). These early flights may have been caused by higher than average mean temperatures throughout New York State in May, although mean temperatures in June, July, and August 1991 were similar to the average (NOAA 1991). All moths were brought to the laboratory and dissected to determine their sex and mating status.

In their original analysis using analysis of variance (ANOVA), Agnello et al. (1996) found no significant edge effect; i.e., there was no difference in the percentage of male, mated female or virgin female moths captured in the three trap locations. In our reanalysis, each bait trap was assigned 1 of 16 directional orientations separated at 22.5° intervals with north = 0°. Each direction was represented by a single trap except for the four corner directions (northeast, southeast, southwest, and northwest), which were represented by three traps each: a center, mid-interior, and edge trap.

We reanalyzed data for each generation (first generation, 22 May to 2 July; second generation, 17 July to 27 August) and for each moth category (male, mated female, and virgin female) separately. For each date in each orchard, we used circular statistics to determine whether the distribution of captured moths was biased in a particular direction.

Circular statistics are commonly used to analyze data that are directional and measured in degrees or are cyclic/periodic in time, such as weeks or months. A characteristic of circular data are that the beginning and end points of the scale are the same, e.g., 0 and 360°, and the starting point can be arbitrary. Calculating the mean of two angles, e.g., 10 and 350°, using linear methods would be inappropriate, because it would give an answer of 180° when the true angular mean is 0°. In circular statistics, the equivalent of the normal distribution is the von Mises distribution, a symmetric unimodal distribution (Fisher 1993). Similar to the normal distribution, which is defined by the mean, μ , and the variance, σ^2 , a measure of dispersion, there are corresponding parameters in circular statistics: the mean angle, μ , and a measure of dispersion, κ (Fisher 1993).

To test whether the mean direction for collected moths showed evidence of a significant ($P \leq 0.05$) directional bias, we used the Rayleigh test, which uses the null hypothesis that the distribution of the data are von Mises (Fisher 1993). The Rayleigh test uses two parameters: θ , the mean angle of collected moths, which ranges between 0 and 360°, and R , a dispersion parameter, which ranges between 0 and 1 and is the length of the mean vector. The higher the R value, the longer the vector and the more tightly concentrated the moths are around θ . P values are calculated using an approximation provided by Fisher (1993).

If the distribution of the moths collected in the bait traps had a significant directional bias using the Rayleigh test, the orchard was split in half using a line perpendicular to θ . Traps were categorized as being in or out of the mean direction half, with an equal number of traps located in the two halves. When θ was not significant, the mean direction for all traps for that date/orchard was considered out. For the corner directions, where there were three traps representing each direction, the mean number captured per trap was used to calculate θ and R .

For example, on 6 June 1991, mated female moths captured in one orchard showed a significant mean directional bias with $\theta = 168^\circ$. The 12 traps located between $\geq 78^\circ$ and $\leq 258^\circ$ were assigned to the in category, and the 12 traps located on the northern half of that orchard between $>258^\circ$ and $<78^\circ$ were assigned to the out category.

The goal of the analysis was to determine whether a directional bias in recaptured moths could affect the ability to detect a significant edge effect. After each trap was categorized as in or out, the total number of male, mated female, and virgin female moths captured in each generation was analyzed to test for an edge effect. Because each trap was repeatedly sampled over time, a generalized estimating equation (GEE) re-

Table 1. Dates when the distribution of obliquebanded leafroller, *C. rosaceana*, adults captured in bait traps in four orchards had a significant directional bias

Date	Orchard	θ (mean direction)	R	P	No. captured
First generation					
6 June					
Mated females	Orchard 1	168° (SSE)	0.92	0.0459	4
10 June					
Mated females	Orchard 1	201° (SSW)	0.36	0.0033	61
13 June					
Males	Orchard 1	144° (SE)	0.35	0.0017	81
Males	Orchard 2	220° (SW)	0.26	0.0061	108
Mated females	Orchard 1	125° (SE)	0.44	≤0.0001	81
17 June					
Mated females	Orchard 1	248° (WSW)	0.52	≤0.0001	69
Mated females	Orchard 2	294° (WNW)	0.76	0.0048	13
Virgin females	Orchard 1	207° (SSW)	0.50	0.0036	37
20 June					
Males	Orchard 1	207° (SSW)	0.68	≤0.0001	32
Mated females	Orchard 1	203° (SSW)	0.63	0.0001	33
Virgin females	Orchard 1	196° (SSW)	0.69	0.0001	30
24 June					
Virgin females	Orchard 1	210° (SSW)	0.68	0.0002	27
1 July					
Mated females	Orchard 4	23° (NNE)	1.00	0.0334	3
Second generation					
22 July					
Males	Orchard 1	203° (SSW)	1.00	0.0070	4
29 July					
Mated females	Orchard 1	182° (S)	0.79	0.0207	3
1 Aug.					
Mated females	Orchard 3	293° (WNW)	0.77	0.0447	5
5 Aug.					
Mated females	Orchard 1	163° (SSE)	0.91	0.0237	6
26 Aug.					
Males	Orchard 1	161° (SSE)	0.93	≤0.0001	13
Virgin females	Orchard 1	187° (S)	0.74	0.0448	6

gression model was used specifying the distribution as negative binomial and using an autoregressive correlation model [PROC GENMOD, dist = negbin, type = ar(1); SAS Institute 2002]. The regression model included Julian date collected, orchard, trap location (center, mid-interior, edge), mean direction (in, out), and all possible two- and three-way interactions that allowed the model to converge to a final solution. Final results show only the *P* values for the minimal model that includes main factors and those interaction terms that were significant. We did not analyze dates when moths were not captured. A Bonferroni correction was used for multiple comparison tests.

In the original analysis, the total 1991 trap catch percentages for the year were used in an ANOVA with an arcsine square-root transformation of the percentages to test for differences between the number of moths captured in the edge, mid-interior, and center of the orchards (Agnello et al. 1996). This analysis found no significant differences (Agnello et al. 1996). Our reanalysis of the data was different in two ways: it considered the two generations separately and it used a GEE regression model. To assess whether differences between our conclusions and those of Agnello et al. (1996) were affected by our use of an alternative statistical method or because of the inclusion of a directional bias in the analysis, we also reanalyzed the data using a reduced model excluding the mean direction factor and testing only the

main effects of date, orchard, and trap location. Results from the reduced and full models were compared to assess the importance of including the mean direction in the analysis.

Results

Males. First-generation males showed a significant bias in their distribution in 3 of 36 possible samples (8.3%): in orchard 1 on 13 and 20 June and in orchard 2 on 13 June (Table 1). Trap location was not significant (Table 2), with similar mean numbers of males captured in the three trap locations (Fig. 1A). Mean direction was a significant factor in the first generation (Table 2), with the average number of males per trap on the half of the orchard that was in the mean direction being significantly higher than the number of males captured in traps classified as out of the mean direction (in = 4.08 ± 3.33 per trap [SD], $N = 36$; out = 0.47 ± 1.45 per trap, $N = 827$; $P \leq 0.001$). The mean direction and trap location interaction term was not assessed because the model did not converge when this term was included (Table 2). Trap location was still not significant when we used the reduced model that included only date, orchard, and trap location.

Second-generation males showed a significant bias in their distribution in 2 of 40 possible samples (5.0%): in orchard 1 on 22 July and 26 August. Trap location

Table 2. Significance of trap location (center, mid-interior, or edge) and mean direction (in or out as defined in the text) on the no. of obliquebanded leafroller, *C. rosaceana*, adults captured per trap

Source	Males		Mated females		Virgin females	
	df	Pr > χ^2	df	Pr > χ^2	df	Pr > χ^2
First generation						
Date	8	≤0.0001	7	≤0.0001	7	≤0.0001
Orchard	3	≤0.0001	3	≤0.0001	3	0.0026
Trap location	2	0.5540	2	0.0017	2	0.1439
Mean direction	1	0.0007	1	0.0928	1	0.0006
Trap × mean direction		NA	2	0.0014		NA
Orchard × mean direction	1	0.0303		NA		NA
Second generation						
Date	9	0.0001	10	0.0074	9	0.2477
Orchard	3	0.0066	3	0.0001	3	0.0342
Trap location	2	0.0144	2	0.0101	2	NS
Mean direction	1	NS	1	NS	1	NS

NA, not applicable, model including this factor did not converge; NS, not significant at $\alpha \leq 0.05$.

was significant in the second generation (Table 2), with more second-generation males captured in the edge and center traps compared with the mid-interior traps (Fig. 1B). Mean direction was not significant, resulting in a reduced model including only date, orchard, and trap location.

Mated Females. First-generation mated females had a significant directionally biased distribution in 7 of 32 possible samples (21.9%): in orchard 1 on 6, 10, 13, 17, and 20 June, in orchard 2 on 17 June, and in orchard 4 on 1 July (Table 1). Trap location was significant, with more mated females captured in the edge traps compared with the mid-interior and center traps (Fig.

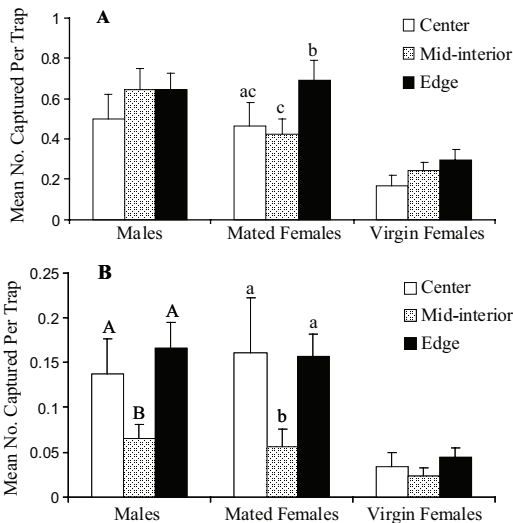


Fig. 1. Distribution of obliquebanded leafroller, *C. rosaceana*, adults captured in center, mid-interior, and edge traps in four pheromone-treated grower orchards studied in 1991. (A) First generation. (B) Second generation. Means with different letters within a generation and sex or mating status category are significantly different at $P \leq 0.05$.

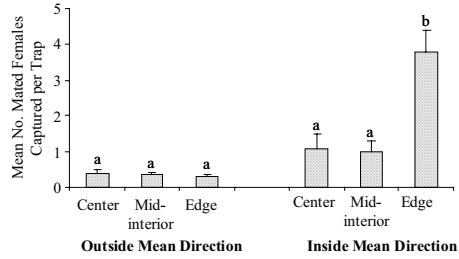


Fig. 2. Distribution of mated female obliquebanded leafroller, *C. rosaceana*, adults in four grower orchards that were divided in half when mated females showed a significant directional bias as described in text. Means with different letters are significantly different at $P \leq 0.05$.

1A). There was also a significant interaction between mean direction and trap location (Table 2). For dates when θ was significant, more mated females were captured in the edge traps compared with the center and mid-interior traps on the half of the orchard that was in the mean direction, but there was no difference between the number of mated females captured in the center, mid-interior, and edge traps located on the half of the orchard that was out of the mean direction (Fig. 2). Trap location was not significant when we used a reduced model that included only date, orchard, and trap location.

In the second generation, mated females had a significant directional bias in their distribution in 3 of 44 samples (6.8%): in orchard 1 on 29 July and 5 August and in orchard 3 on 1 August (Table 1). Similar to second-generation males, trap location was significant (Table 2), with more second-generation mated females captured in the edge and center traps compared with the mid-interior traps (Fig. 1B). Mean direction was not significant, resulting in the reduced model including only date, orchard, and trap location.

Virgin Females. First-generation virgin females had a significant bias in their distribution in 3 of 32 samples (9.4%): in orchard 1 on 17, 20, and 24 June (Table 1). Like first-generation males, trap location was not significant, with similar mean numbers of virgin females captured in the three trap locations (Fig. 1A), and mean direction was significant (Table 2), with more virgin females captured in traps located in the half of the orchard that was in the mean direction than were captured in traps classified as out of the mean direction (in = 2.33 ± 2.54 per trap, $N = 36$; out = 0.15 ± 0.51 per trap, $N = 731$; $P \leq 0.001$). When we used a reduced model including only date, orchard, and trap location, trap location was still not significant.

Second-generation virgin females had a significant bias in their distribution in 1 of 40 samples (2.5%): in orchard 1 on 26 August (Table 1). Neither trap location nor mean direction was significant for second-generation virgin females (Table 2; Fig. 1B).

Discussion

Our reanalysis of the 1991 data from Agnello et al. (1996) showed that a directional bias in the spatial

distribution of recaptured moths in an orchard can affect the ability to detect a statistically significant edge effect. When the directional bias in the distribution of first-generation mated females was taken into account, the results showed that significantly more mated females were captured in the edge traps. We detected no significant edge effect when this biased distribution was not taken into account. For second-generation moths, there was no evidence that a biased directional distribution affected the analysis results, but we did find that the number of mated females and males was significantly higher in the edge and center traps compared with the mid-interior traps. In contrast, the spatial distribution of virgin females between edge, mid-interior, and center traps was uniform in both the first and second generations.

Agnello et al. (1996) did not find a statistically significant edge effect for mated females using ANOVA, and they concluded that mated females were uniformly dispersed in the study orchards. Our results suggest that using a more sensitive analytical method that includes directional information in the analysis and separating the generations before analyzing them can show more of the spatial pattern than using an ANOVA and analyzing both generations together.

The data collected by Agnello et al. (1996) in 1991 provided information on the spatial distribution of moths, but their study was not designed to give any insight into the causal factors. The mean direction of mated females was most frequently significant in orchard 1, with θ values ranging between 125 and 248° (southeast-southwest). Due north of orchard 1 was forested land, to the east was a paved road, due south was a field road and another apple orchard that was not treated with pheromone, and to the west were apple trees that were not part of the study plot and were not treated with pheromone (Fig. 3). We suggest some possible mechanisms that may be contributing and interacting to result in the biased spatial distribution patterns we found for mated females in orchard 1.

First, significantly more mated females were captured in edge traps in both the first and second generations across all four orchards, a pattern that could reflect high levels of mated female immigration. Higher numbers of mated females along the southern edge of orchard 1, specifically, could result from biased immigration into this orchard by mated females originating from the orchard south of orchard 1. We did not have access to detailed historical weather data for orchard 1 but winds, in general, are west-southwest in this region of New York in June, when first-generation moths are active (NOAA 1998). If mated females disperse in a biased direction downwind, mated females emigrating from the orchards south of orchard 1 would contact the southern border of orchard 1 first, increasing the number of mated females along the southern edge.

Higher numbers at the southern edge traps could also result from biased directional emigration of mated females within orchard 1 upwind, away from the high levels of synthetic pheromone released in orchard 1.

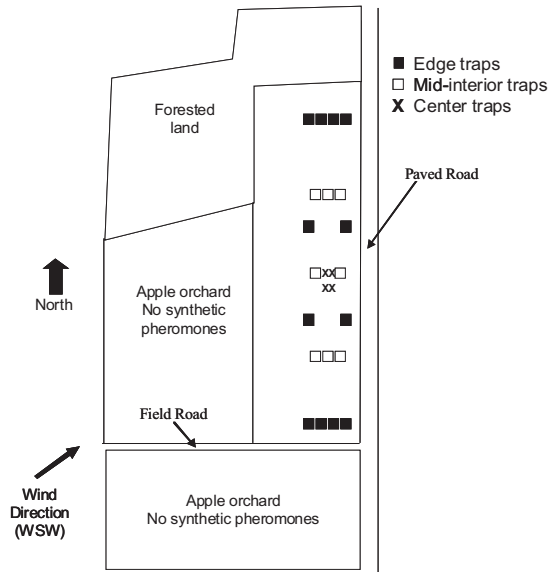


Fig. 3. Map of orchard 1 (not drawn to scale). Small arrow indicates average wind direction in June in this region of New York.

Mated female spruce budworms, *Choristoneura fumiferana* (Clem.) (Tortricidae), increase their flight activity when exposed to synthetic pheromone (Sanders 1987), and the proportion of female light brown apple moths, *Epiphyas postvittana* (Walk.) (Tortricidae), that fly increases with increasing population density (Danthanarayana 1976). Using electroantennogram (EAG) measures, Gokce et al. (2007) showed that female obliquebanded leafroller adults can perceive their own sex pheromone. Mated female leafrollers may increase their flight activity in response to high pheromone concentrations, or they could interpret higher levels of pheromone as an indication of a higher population density and increase their flight activity. An increase in flight activity does not necessarily result in a biased directional distribution, but if mated females have a preference for upwind flight under high concentrations of pheromone, this could result in a spatial distribution pattern with more mated females emigrating toward the southern edge of orchard 1.

The spatial distribution of virgin females in orchard 1 may be a third possible factor determining the distribution of mated females. There was a significant southern bias in the spatial distribution of first-generation virgin females captured in orchard 1: $\theta = 196-210^\circ$. Higher populations of virgin females in the southern trees could result in higher subsequent populations of mated females, which would help explain the overall biased southern distribution of mated females.

However, this does not completely explain the spatial distribution of mated females, because virgin females were distributed evenly between the edge, mid-interior, and center traps in the south, whereas significantly more mated females were located in the

edge traps. This secondary finer-scale spatial pattern could result from a fourth possible mechanism: higher mating success along the southern edge of the orchard, possibly caused by lower synthetic pheromone concentrations. Pheromone concentrations along a transect between a pheromone-treated and an untreated apple orchard were shown to decline in the pheromone-treated orchard up to 20 m from the border when the wind was blowing obliquely from the untreated side (Milli et al. 1997). Witzgall et al. (1999) found significantly lower pheromone concentrations in border trees at the upwind edge of an orchard in pheromone-treated orchards. The southern edge of orchard 1 is the upwind side, and higher mating success along this edge caused by lower synthetic pheromone concentrations could result in higher numbers of mated females in the southern edge traps.

The last possible mechanism we present is a reflecting boundary reaction (Schtickzelle and Baguette 2003). If mated females detect a change in the environment when dispersing from orchard 1 into the field road south of orchard 1, and, in response, return to orchard 1, this would increase their overall flight activity in the southern edge of the orchard, increasing the probability of a higher trap catch along the southern edge compared with the mid-interior and center traps. A reflecting boundary could also affect mated female dispersal behavior along the north and east edges of orchard 1, which border forest and a paved road, but there may have been too little flight activity in these sections to show a significant edge effect given that there were significantly more mated females captured in the southern end of the orchard.

Considerable research shows that males of many species of moths fly upwind in the presence of pheromones (Cardé and Willis 2008). Considerably less is known about whether mated female moths respond to wind direction, and, if they do, whether their response is different in the presence or absence of high concentrations of pheromone. Additional field and laboratory studies are necessary to determine which, if any, of these possible mechanisms are affecting the flight behavior of mated females and the mating success of virgin female moths. A better understanding of mated female dispersal behavior would be particularly useful because mated female immigration is still considered one of the most important factors affecting the success of pheromone disruption control programs (Cardé and Minks 1995).

Our analysis results also suggest that there are differences in the spatial distribution patterns of moths as a function of sex and mating status. Mated females in both the first and second generations showed a biased directional distribution more frequently than did either males or virgin females. In contrast, data from mark-release-recapture field studies where moths were released from a single site in an apple orchard that had no synthetic pheromones showed that recaptured male leafrollers were more likely to have a significant directionally biased distribution than either mated or virgin females (Hsu 2002). An upwind bias in dispersal is commonly found in males responding to

pheromone plumes in the presence of wind (Cardé and Willis 2008). When exposed to homogeneous pheromone environments, however, studies show that males in two related species of tortricids, the summerfruit tortrix, *Adoxophyes orana* (Fischer von Röslerstamm), and the oriental fruit moth, *Grapholita molesta* (Busck), cease their biased upwind flight behaviors (Kennedy et al. 1981, Willis and Baker 1984). All four orchards used in 1991 were treated with synthetic pheromone, and this might explain why so few of the male data sets from 1991 showed a significant directional bias in their spatial distribution while males in an untreated orchard often had a significant directionally biased distribution.

An additional insight gained from our reanalysis is evidence that the dispersal behavior of first- and second-generation moths might be qualitatively different: there was no significant directional bias in the distribution of second-generation males, mated females, or virgin females in the 1991 study, but mean direction was a significant factor alone or as an interaction term for all three categories of moths in the first generation. In addition, there was no significant difference in the number of moths captured in the edge, mid-interior and center traps for first-generation males, but in the second generation, significantly more males were captured in the edge and center traps compared with the mid-interior traps. The possibility that first- and second-generation adults have consistently different dispersal behaviors is worth exploring in future studies. Alternative control measures targeting immigrating mated females might be more successful in the first than in the second generation if additional evidence suggests that the edge effect is caused by mated female immigration. Likewise, pheromone control might be more successful with second-generation adults if the total number of second-generation mated females immigrating into pheromone-treated orchards is lower.

Unfortunately, there are no historical records of trap catch data using bait pails that can be used to compare the population captured in 1991 with other years, but we believe the population captured in 1991 was not unusual. Consecutive years of pheromone trials in Orleans and Wayne Counties between 1989 and 1999 show that obliquebanded leafroller populations vary considerably from year to year and between orchards. Pheromone trap catch numbers, infestation levels, and damaged fruit levels found in 1991 were well within the bounds of variation observed over this 10-yr period (A.M.A. and W.H.R., unpublished data).

After 4 yr of pheromone trials, Agnello et al. (1996) concluded that the effectiveness of a pheromone disruption control strategy needed to be tested at a much larger scale than was used in their studies. Our reanalysis results support this general conclusion. We found significantly more first- and second-generation mated females in edge traps, suggesting that the immigration potential of mated females may be operating at a larger spatial scale than the size of the pheromone-disrupted plots. More recent studies applying pheromones on an area-wide basis, where the perimeter:

area ratio is lower, have shown improved efficacy against codling moths, *Cydia pomonella* L., and oriental fruit moths in the northwestern United States: Michigan and Pennsylvania (Brunner et al. 2001; Il'ichev et al. 2002; Calkins and Faust 2003; Gut et al. 2004; Epstein et al. 2007; Hull et al. 2007, 2008). Tests of area-wide pheromone disruption targeting oblique-banded leafrollers have not been conducted but could show similar results.

Including a directional analysis into tests for edge effects is not difficult if enough traps are associated with each angular direction. In all of the studies conducted by Agnello et al. (1996) between 1989 and 1992, only the data from the 1991 study was appropriate for this type of analysis because the traps were arranged in three concentric rings within the orchard. Data collected using transects are generally not amendable to a circular analysis unless there are transects in at least the four cardinal directions in the same study plot.

Circular statistics are a relatively simple and powerful tool, and an analysis of any type of spatial distribution or dispersal data can benefit from identifying a directional bias, which can suggest new hypotheses to be tested. The Rayleigh test can be done using a spreadsheet or commercially available software, and there is a growing body of literature to guide users in more advanced analyses, such as hypothesis testing, regression, and prediction (Batschelet 1981, Fisher 1993, Jammalamadaka and SenGupta 1998, Presnell et al. 1998, Lund 1999, Mardia and Jupp 2000, Jammalamadaka and SenGupta 2001, Downs and Mardia 2002, Ghosh et al. 2003).

In addition to analyzing spatial distribution patterns, the field of entomology has benefitted from the use of circular statistics to study orientation behavior in the presence or absence of odors (Brady and Griffiths 1993; Evans and Allen-Williams 1993, 1994; Guevara et al. 2000; Otálora-Luna et al. 2004), orientation in response to magnetic fields and polarized light (Havukkala and Kennedy 1984, Shen et al. 1998, Banks and Srygley 2003, Stalleicken et al. 2005), foraging behavior to locate hosts, habitat, or mates (Toepfer et al. 1999, Durier and Rivault 2000, Fourcassié and Oliveira 2002, Szentesi et al. 2002, Kost et al. 2005), and dispersal in general (Hsu 2002, Morse 2002, Desouhant et al. 2003, Roux et al. 2006). Additionally, studies in insect physiology (Yetman and Pollack 1987, Dean 1992, Pfeiffer et al. 2005) and circadian rhythms (Gimenes et al. 1996, Klarsfeld et al. 2003, Chahad-Ehlers et al. 2007) have used circular statistics.

In conclusion, we showed that the ability to detect a statistically significant edge effect in oblique-banded leafroller adults in apple orchards is sensitive to whether there is a directional bias in the spatial distribution of the moths and to analyzing the generations separately. We recommend that these factors be considered when testing for edge effects in future studies. We have also introduced the use of circular statistics and GEE regression models as tools that could be used in other studies where the data have a

directional component, do not follow a normal distribution, and are collected repeatedly over time.

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