

The Distribution of European Corn Borer (Lepidoptera: Crambidae) Moths in Pivot-Irrigated Corn

SCOTT C. MERRILL,^{1,2} SHAWN M. WALTER,³ FRANK B. PEAIRS,⁴ AND ERIN M. SCHLEIP⁵

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ABSTRACT The European corn borer, *Ostrinia nubilalis* (Hübner), is a damaging pest of numerous crops including corn, potato, and cotton. An understanding of the interaction between *O. nubilalis* and its spatial environment may aid in developing pest management strategy. Over a 2-yr period, ≈8,000 pheromone trap catches of *O. nubilalis* were recorded on pivot-irrigated corn in northeastern Colorado. The highest weekly moth capture per pivot-irrigated field occurred on the week of 15 July 1997 at 1,803 moths captured. The lowest peak moth capture per pivot-irrigated field was recorded on the week of 4 June 1998 at 220 moths captured. Average trap catch per field ranged from ≈1.6 moths captured per trap per week in 1997 to ≈0.3 moths captured per trap per week in 1998. Using pheromone trap moth capture data, we developed a quantified understanding of the spatial distribution of adult male moths. Our findings suggest strong correlations between moth density and adjacent corn crops, prevailing wind direction, and an edge effect. In addition, directional component effects suggest that more moths were attracted to the southwestern portion of the crop, which has the greatest insolation potential. In addition to the tested predictor variables, we found a strong spatial autocorrelation signal indicating positive aggregations of these moths and that males from both inside and outside of the field are being attracted to within-field pheromone traps, which has implications for refuge strategy management.

KEY WORDS *Ostrinia nubilalis*, spatial, pheromone, predictive model, distribution

Stem-boring Lepidoptera damage numerous cereal crops including rice, corn, sorghum, and millet (Harris 1990, Kfir et al. 2002). In the United States, the 90+ million acres of corn planted annually (U.S. Department of Agriculture–National Agricultural Statistics Service [USDA–NASS] 2011) are vulnerable to stem-boring pests, and thus, substantial control costs are incurred annually (Mason et al. 1996). For example, before widespread adoption of *Bacillus thuringiensis* (*Bt*) corn, the European corn borer, *Ostrinia nubilalis* (Hübner), cost producers approximately US\$1 billion annually in the United States alone (Mason et al. 1996).

Control tactics for stem borers are numerous and include pesticide applications against adults or larvae, cultural controls (e.g., crop rotations), mating disruption using pheromone lures, and transgenic insecticidal cultivars (e.g., cultivars with insecticidal *Bt* transgenes) (Mason et al. 1996, Gould 1998, Kfir et al. 2002, Alfaro et al. 2009). In addition, strategies combining sterile insect releases, transgenic crops, and refuge

strategies may provide increased control of some of our important lepidopteran pests (Tabashnik et al. 2010). The success of resistance management through high-dose refuge strategies (Alstad and Andow 1995) is largely dependent on the dispersal and mating behavior of the targeted pest (Gould 1998, Ives and Andow 2002, Bailey et al. 2007). Effective resistance management requires the use of multiple control tactics, and thus, novel tactics are sought to augment or replace current tactics, especially those tactics that are likely to be overcome by pests or lead to increased resistance prevalence (e.g., replacing broadcast pesticide applications with site-specific pesticide management).

Understanding the spatial population dynamics and movement of pests helps develop strategies for controlling stem-boring pests (Harris 1990) and optimize refuge strategies (Cerdeira and Wright 2004). Spatial distributions of animals are usually described by their aggregation or degree of nonrandomness, making the number of samples taken and distance between sampling sites important. If individuals are independently dispersed across a field then sampling a small area or using a small number of samples would be reasonable. However, it is more likely that individuals will not be independently dispersed over space. Indeed, pest distribution patterns are typically heterogeneous (Taylor 1984). For example, distinct patterns in western bean cutworm, *Striacosta albicosta* (Smith), moth abun-

¹ Department of Plant and Soil Science, 63 Carrigan Drive, 217 Jeffords Hall, University of Vermont, Burlington, VT 05405-0082.

² Corresponding author, e-mail: scott.c.merrill@UVM.edu.

³ 312 Diamond Drive, Fort Collins, CO 80525.

⁴ Department of Bioagricultural Sciences and Pest Management, Colorado State University, Fort Collins, CO 80523.

⁵ Department of Statistics, Colorado State University, Fort Collins, CO 80523.

dances were found in pivot-irrigated corn in northern Colorado (Merrill et al. 2011). *O. nubilalis* moths consistently settled in some areas more frequently than others (Hunt et al. 2001, Showers et al. 2001, Bailey et al. 2007). More pest samples may be required to determine pest distributions adequately for application of spatially explicit management tactics, but sampling effort will have to be balanced against the time and resource constraints of pest management decision makers.

One of the most important stem-boring lepidopteran pests is *O. nubilalis*, the European corn borer. This pest damages many crops including cotton, wheat, and potato, and is considered one of the most devastating pests of corn (Derrick et al. 1992, Mason et al. 1996, Kfir et al. 2002). The biology and ecology of *O. nubilalis* has been well studied (e.g., Mason et al. 1996). Control of this pest, and many other stem-boring pests, is complicated because much of the pest's life cycle is spent protected within crop stem tissue. Thus, pesticide applications, if necessary, should be timed to coincide with the short window between egg-hatch and when the larvae bore into the plant (Mason et al. 1996). Control may be simplified using transgenic crops such as *Bt* corn. Extensive *Bt* crop use has resulted in dramatic area-wide suppression of *O. nubilalis* across corn-producing regions in the United States (Hutchison et al. 2010). However, although resistance to *Bt* crops may be delayed with effective management (Alstad and Andow 1995, Ives and Andow 2002), heritable resistance to *Bt* toxins (Cry1Ab) currently exists in *O. nubilalis* populations (e.g., Crespo et al. 2009) and eventually will become more widespread (Alstad and Andow 1995, Ives and Andow 2002). Thus, deployment of novel tactics for control of *O. nubilalis* will become necessary.

Studying the behavioral ecology of *O. nubilalis* moths may lead to the development of novel tactics to help control this species or improve our resistance-management strategy. Although research has described mating and oviposition behavior, understanding the small scale within-field spatial distribution of male *O. nubilalis* moths has seen little attention. We sought to elucidate some of the variables influencing the distribution of male European corn borer moths in sprinkler-irrigated corn. Male moths are influenced by sexual attractants (e.g., Klun and Robinson 1971, Sole et al. 2008), and females typically emit sexual attractant pheromones starting at ≈ 2000 hours with activity continuing through until dawn (Mason et al. 1996). Thus, conditions influencing the dispersion of these pheromones, such as wind, may influence detection and tracking by male moths (Turner et al. 1978, Mafra-Neto and Carde 1994, Bau et al. 1999, Showers et al. 2001). The direction of the effect of the prevailing wind direction is complicated. Specifically, if males are obligatorily leaving the field during their mating search, then returning to the field, pheromone traps on the downwind side of the field would be the first encountered by the searching males. Conversely, if males emerge and fly toward the first detected pheromone plume, more males should be detected on the

upwind side of the field (i.e., the probability of arriving at an upwind site is much higher than a downwind site, and thus, a moth emerging within the field will be more likely be trapped in an upwind trap.) In addition to wind, *O. nubilalis* mating behavior has been linked to within-field plant elevation. For example, tall plants or high points are considered attractive mating action sites (Mason et al. 1996). Distance from alternate population sources (e.g., other corn fields or nearby grassy areas) or distance from field edges may be associated with higher moth activity (Sappington 2005, Bailey et al. 2007). Directional effects such as an insolation effect (or as an effect of increased insolation such as decreased moisture availability, increased temperatures, or increased temperature fluctuations) may influence moth distribution (Loughner and Brindley 1971, Royer and McNeil 1993). Using these variables, we sought to determine whether spatial patterns exist in the distribution of *O. nubilalis* in pivot-irrigated corn in a semiarid region. Moreover, we hypothesized that additional spatial aggregation effects may exist beyond those tested by our predictor variables. Ideally, an increased understanding of moth distribution patterns may help direct pheromone trap placement for monitoring *O. nubilalis* population dynamics (Derrick et al. 1992), assist in refuge management strategy, and potentially, aid in the development of novel control tactics.

Materials and Methods

O. nubilalis flights were monitored during the 1997 and 1998 growing seasons in two center pivot-irrigated corn fields near Wiggins, Morgan County, CO (Field 1: 40.332104 N, 104.02997 W; Field 2: 40.30156 N, 103.946976 W). Pivot-irrigated field sites, each measuring ≈ 89 ha, and adjacent corn fields were planted as part of a continuous corn cropping system. The two fields were chosen based on cooperator interest in precision farming and variability in terrain. Samples were collected for 2 yr. In 1997, 10 weekly *O. nubilalis* samples were collected on Field 1 from 24 June to 8 September and eight weekly *O. nubilalis* samples were collected on Field 2 from 15 July to 3 September. In 1998, 13 weekly samples were collected on Fields 1 and 2 from 4 June to 26 August.

We used pheromone traps to sample for *O. nubilalis*, which were traps similar to those described by Thompson et al. (1987) and consisted of a 3.785-liter (1 gal) plastic milk jug with a pheromone lure attached to the underside of the cap with 10 ml of *cis*-11-tetradecenyl acetate (*cis*-11-14:Ac, 1:0 *cis*:*trans*) (Klun and Robinson 1971). Traps were filled with 1,500 ml of soapy water (mixed at a rate of two drops liquid dish soap to 1 liter of water (Doyle 1994)). Male *O. nubilalis* moths were removed from the trap, recorded, and discarded in the field on a weekly basis. During weekly trap counts, water that had evaporated from the traps was replaced to the previous level. Traps were placed in Field 1 on 17 June 1997 and in Field 2 on 8 July 1997. Traps were removed on 8 September 1997 after moth flight ceased. Pheromone

lures were replaced monthly. In 1998, *O. nubilalis* traps were placed in Field 1 and Field 2 on 28 May and removed on 26 August. Traps were initially placed on the ground. After cultivation operations were complete, the traps were placed on the electric fence posts. Pheromone lures were replaced monthly.

Each field was sampled using a coarse grid sampling pattern of 76.2 by 76.2 m² overlaying the pivot-irrigated field. Coarse grid samples were taken at a rate of one per grid square. Traps were placed within the corn row. Traps were located in the same positions in the field in both years. In 1997, samples were collected at 91 and 100 coarse grid points on Field 1 and Field 2, respectively. In 1998, samples were collected at 86 and 100 coarse grid points on Field 1 and Field 2, respectively. The number of samples necessary for determination of spatial patterns useful for field management of the European corn borer is unknown. That is, to determine spatial patterns (e.g., spatial autocorrelation and distribution), a range of distances between traps was needed (Turner et al. 2001). Grid-based sampling was augmented with additional traps as follows: In both fields, one quadrant had two additional pheromone traps placed within each grid square. In the remaining three quadrants, one additional trap was placed within each grid square. Field 1 had 98 and 95 additional samples collected in 1997 and 1998, respectively. Field 2 had 86 and 78 extra samples in 1997 and 1998, respectively. A restriction on the random location of these traps was that they had to be at least 30 m apart to minimize inter-trap interference (Mason et al. 1996). Sufficiency of inter-trap interference reduction was tested by determining whether moth abundance per trap in the high trap density quadrant was lower than in the low trap density quadrants. In total, there were 375 trapping locations on the two fields in 1997. In 1998, because of planting differences, the number of trapping locations was reduced to 359. All sampling points were referenced with global positioning system (GPS) technology using OmniStar 6300 or OmniStar 7000 differential (OmniStar Inc., Houston, TX).

Weekly trap captures were averaged by sampling point across each field season and used as the dependent variable. The following independent variables were regressed against the *O. nubilalis* counts: 1) the distance from the edge of the field (meters), 2) whether the nearest adjacent crop was continuous corn or other, 3) elevation, 4) prevailing wind direction effect, and the directional variables, 5) North-South component (NS), 6) East-West component (EW), 7) and the interaction term NS × EW. To examine the effect of the distance of the trap to an alternative population source, we used an indicator variable labeled "corn adjacent." A corn adjacent value of 1 indicated that the nearest adjacent crop was corn (i.e., a likely population source) and 0 if it was something other than corn (e.g., fallow, alfalfa, etc.). The directional (anisotropic) variables, NS component, EW component, and the interaction term between NS × EW components were calculated in meters using UTM coordinates. The prevailing wind

direction variable was calculated using hourly Colorado Agricultural Metrological Network (Andales et al. 2009) wind direction data (in degrees), from 2000 to 0500 hours at each site during the sampling period for each year. Hourly wind direction data were binned by increments of 5°. For each site and each year, the bin with the largest count was considered the nighttime prevailing wind direction. Nighttime wind direction data were messy, with two apparent peaks occurring at ≈300 and 100° at both sites during each year. Using 5° increments, the nighttime prevailing wind direction was found to be 140° for field 1 in 1997 (i.e., wind was blowing primarily southeasterly) and 310° (wind was blowing primarily northwesterly) for field 2. In 1998, the nighttime prevailing wind was found to be 100° on field 1 and 110° on field 2. Male moths are expected to fly upwind to trace the pheromone plume of potential mates. Therefore, the prevailing wind effect at each trap location was calculated as follows:

Field 1 in 1997: Prevailing wind at 140° = 1.192 × NS – EW

Field 1 in 1998: Prevailing wind at 100° = 0.176 × NS – EW

Field 2 in 1997: Prevailing wind at 310° = EW – 0.839 × NS

Field 2 in 1998: Prevailing wind at 110° = 0.363 × NS – EW

where EW and NS are the East-West and North-South components measured in meters from the center of the field, respectively. Using Field 1 in 1997 as an example, because the nighttime prevailing wind effect increased as within-field trap location increased toward the northwest (i.e., opposite its 140° source), a location 30 m west of the center of the pivot and 30 m north of the center would have a high prevailing wind effect calculated as: 1.192 × 30 – (–30) = 65.76, as contrasted with a point toward the downwind side of the field, 30 m east and 30 m south calculated as: 1.192 × (–30) – 30 = –65.76. Wind speed was not addressed during the calculation of prevailing wind direction effect. However, Showers et al. (1995) suggest that moth movement is limited when wind speed exceeds ≈8 km/h. If high winds were associated with a predominant direction that differed from wind patterns during periods of relatively low wind speeds then a measure of the prevailing wind direction effect including all wind speed observations may not accurately reflect moth behavior. However, during our study, high winds were not associated with a predominant direction, and while the prevailing wind direction effect may have shifted slightly with the removal of high wind observations (on average ≈10°), we feel it is unlikely that removing these high wind speeds would more accurately represent moth behavior or affect our results.

High points within corn fields have been associated with increased attractiveness as mating sites (Mason et al. 1996). Within-field elevational differences were quantified using a USGS Digital Elevation Map (30 m grid size).

Because an analysis of between-year and between-field variation was beyond the scope of this research, we accounted for between-year and between-field variation using indicator variables. That is, we corrected for spatial dependence of moth abundance between fields and between years.

A set of a priori candidate models was developed using all subsets of the variables of interest (distance from edge of field, corn adjacent, elevation, prevailing wind direction effect, NS component, EW component, and the interaction between the NS × EW components) (GLMulti package, R Development Core Team 2008). To reduce model selection bias, an information-theoretic approach to model selection and multimodel inference was used (Burnham and Anderson 2001, 2002, 2004). For model selection, we first computed the statistic AICc *L*, based on the corrected Akaike’s Information Criterion, which provides a measure of the likelihood that the selected model is the best candidate model given the data (Burnham and Anderson 2002, 2004). We considered strong candidate models to be those with AICc *L* > 0.05. These models were then used for multimodel inference. The various candidate models were assigned weights using weighted AICc values, AICc *w_r*, (Burnham and Anderson 2002, 2004). For example, if two candidate models were selected as being good candidate models, with model 1 having an AICc *w_r* of 0.7 and model 2 having an AICc *w_r* of 0.3 (weights add to 1), then values calculated using model 1 would have a weight of 0.7, while model 2’s values would have a weight of 0.3. The model-averaged result was transformed into a spatial trend surface using the Raster Calculator tool in ArcMap 9.3 (ESRI 1999–2008).

Variation in moth distribution that is not explained by our predictor variables may be associated with aggregation behavior (i.e., spatial autocorrelation may exist in moth capture patterns). We used the statistical R packages (gstat, spatial, geoR, and ape) to examine our data for spatial autocorrelation and incorporate these spatial patterns into our model-averaged regression results (R Development Core Team 2008). Specifically, we tested for spatial autocorrelation within the residuals from the selected candidate models using Moran’s (1948) contiguity ratio (also known as Moran’s *I*). If spatial autocorrelation was found, it was quantified using variograms (Cressie 1993) fit to exponential, spherical, or Gaussian covariance functions. The variogram with the best fitting covariance function (i.e., lowest residual sum of squares) was used to provide the spatial parameters: range, sill, and the nugget effect. The range parameter is used to describe the distance at which moth trap catch data are no longer spatially correlated (Plant 2012). The sill represents the long range (across-field) variability remaining in the residuals. The nugget effect represents sampling error or short-range variability (i.e., variability at a sample point). Using these spatial parameters, we calculated an interpolated surface (kriged interpolated surface; Cressie 1993) for each of the selected candidate models. The kriged interpolated surfaces were then averaged using the AICc *w_r* of the associ-

Table 1. Summary statistics for year and field

Data type	Year 1997		Year 1998	
	Field 1	Field 2	Field 1	Field 2
Peak catch date	24 June	15 July	4 June	4 June
Peak catch abundance	1,374	1,803	275	220
Total caught	3,116	2,159	774	708
Average per trap	16.5	11.9	4.3	4.0
Average per trap per week	1.7	1.5	0.3	0.3

ated model, resulting in a model-averaged kriged estimate. The model-averaged kriged estimate was written to a spatial layer (rgdal package, R Development Core Team, 2008) and added to the model-averaged regression surfaces using the Raster Calculator tool in ArcMap 9.3 (ESRI 1999–2008). The resulting maps (i.e., maps for each field for each year) modeled the distribution of male *O. nubilalis* moth density across the pivot-irrigated corn system.

To measure the explanatory power of each of the predictor variables, we assigned a variable relative importance weight. This weight was calculated as the sum of the AICc *w_r*s over all models in which the predictor variable occurred. These weights can then be compared between the predictor variables to determine relative importance (Burnham and Anderson 2002, 2004). These weights can range from 0 to 1, with higher values indicating the variable being more important in predicting the response. Because variable weights are derived from AICc *w_r*s, they can be interpreted as the likelihood of the predictor variable being an important predictor variable for understanding spatial variation in *O. nubilalis* moth density.

Results

Ten weekly *O. nubilalis* samples were collected in 1997 on Field 1 from 24 June to 8 September and eight weekly *O. nubilalis* samples were collected on Field 2 from 15 July to 3 September. Thirteen weekly samples were collected on both Fields 1 and 2 in 1998 from 4 June to 26 August. Seven hundred and twenty-five pheromone traps were used to obtain the weekly moth capture averages. From that total, 42 traps recorded zero *O. nubilalis* during a field season. A high of 58 moths was captured in a single trap on Field 2 in 1997. *O. nubilalis* flights in these two seasons would be considered larger than normal based on moth catches at six black-light traps located between the study fields and the Kansas border. The 1997 and 1998 season totals for these traps averaged 225 and 130% of the rolling 10-yr average, respectively (S. D. Pilcher and F.B.P., unpublished data). Summary statistics (Table 1) are given for each year and each field for the peak catch date and amount, the total moths caught, and the average moths caught per trap, and per trap per week. It is interesting to note that a second smaller peak was noted in both years and is small in comparison with the overall number of insects collected. However *O. nubilalis* second-generation flight is often larger than the first flight in eastern Colorado (Walter et al. 2000).

Table 2. Candidate models selected for multimodel inference and their residual spatial components

Rank	Predictor variables ^a	Model fit statistics					Fitted spatial parameters ^b		
		AICc	ΔAICc	AICc L	AICc w _r	Adj. R ²	Range	Sill	Nugget
1	FY, DE, CA, EW, NS, PW, EW*NS	1584.44	0	1	0.53	0.451	769.73	0.593	0.287
2	FY, CA, EW, NS, PW, EW*NS	1586.39	1.94	0.38	0.20	0.449	598.57	0.521	0.279
3	FY, DE, CA, EW, NS, PW, EW*NS, elevation	1586.48	2.04	0.36	0.19	0.450	776.11	0.597	0.287
4	FY, CA, EW, NS, PW, EW*NS, elevation	1588.23	3.79	0.15	0.08	0.448	599.35	0.520	0.279

^a FY, field/year indicator variable; CA, variable corn adjacent; DE, variable distance from the edge of the field; NS, North–South component; EW, East–West component; and PW, prevailing wind direction effect.

^b Spatial parameters were calculated using the exponential covariance function.

Furthermore, more *O. nubilalis* were collected in 1997 in both fields.

Four candidate models were selected as good models for predicting the prevalence of male *O. nubilalis* moths in pivot-irrigated corn (Table 2) and were averaged using their AICc w_s. Coefficients for the model-averaged regression model can be found in Table 3. The model-averaged regression model was used to estimate variation in field level abundances captured by the predictor variables. The model-averaged regression model was mapped using the map calculator tool in ArcMap 9.3 (ESRI 1999–2008) (e.g., Fig. 1).

Corn adjacent and the prevailing wind effect variables were included in all of the selected candidate models, indicating that these are both strong variables for predicting prevalence of *O. nubilalis* moths (Table 3). The coefficient for corn adjacent was positive, indicating that more moths were found in traps located near adjacent corn fields rather than other adjacent crops. Prevailing wind direction effect indicated that more moths were found in traps on the upwind side of the fields. In addition, the directional variables, EW, NS, and EW × NS components were included in all of the selected candidate models. Collectively, these variables indicate that more moths were found on the southwestern side of the fields. The variable distance from the edge of the field was found in two of the four models giving it a variable weight of 0.72. The coefficient estimate indicated that more moths were found around the edge of the field than in the center. Elevation was a variable in two of the four models, although it resulted in a weaker relative variable weight of 0.27. Elevation appears to have a negative effect on moth prevalence, although this is opposite of what we would expect.

Table 3. Variable relative importance values

Predictor variable	Estimate	SE	Weight	Effect direction
Intercept (Field 1 1997)	1.950	0.207	1.00	+
Field 1 1998	-1.020	0.0831	1.00	-
Field 2 1997	0.230	0.0891	1.00	+
Field 2 1998	-0.314	0.0899	1.00	-
Corn adjacent	0.190	0.0648	1.00	+
EW component	-0.001	0.000322	1.00	-
NS component	-0.001	0.000313	1.00	-
Prevailing wind	0.000356	0.000115	1.00	+
NS × EW component	0.0000021	0.0000006	1.00	+
Distance from edge	-0.000373	0.000322	0.72	-
Elevation	-0.000062	0.0136	0.27	-

A strong positive spatial autocorrelation signal was found in the residuals of the selected candidate models (Moran's I: *P* value < 0.0001), indicating that moths are aggregating spatially (Fig. 2). The spatial autocorrelation was quantified using a variogram for each of the four selected candidate models (Cressie 1993). For every model, the covariance function that best fit the variogram was the exponential covariance model. The spatial parameters, range, sill, and nugget effect, were fit using the exponential covariance function (Table 2). Figure 3 depicts the modeled distribution of *O. nubilalis* moths on Field 2 during the 1997 field season.

The SDs of the regression coefficients are unconditional on the selected model, that is, the SDs resulting from model averaging encompass both the variation in the estimates themselves as well as a component for model selection uncertainty. When a variable is not selected to be significant in one of the chosen models, the coefficient for that variable for that model is set to 0. This results in an increase in the standard deviation for coefficients of variables that are not included in all of the chosen models. This is apparent with the distance from the edge of the field variable in our model. This variable was selected as significant in the AICc-selected best model and thus, considered an important predictor of moth distribution. However, because the predictor was not selected in all four candidate models, the resulting model-averaged coefficient estimate and standard error are -0.00373 and 0.000322, respectively. Therefore, the 95% CI for the coefficient for distance from the edge of the field includes 0.

Discussion

Strong spatial correlation was found in the *O. nubilalis* trap catch data. Although we should not assume that the spatial distribution of male moth catches directly correlates to the location of female moths or attractive oviposition sites, the location of male moths does provide information about mating behavior. Thus, there are important implications for both refuge management and mating-disruption strategies.

Supporting previous research, trap catches were greater near corn fields (e.g., Sappington 2005, Bailey et al. 2007) and diminished adjacent to crops not known to be quality hosts for *O. nubilalis* (i.e., two of the crops adjacent to the tested field sites were sugar beet and onion; these crops are not known to suffer

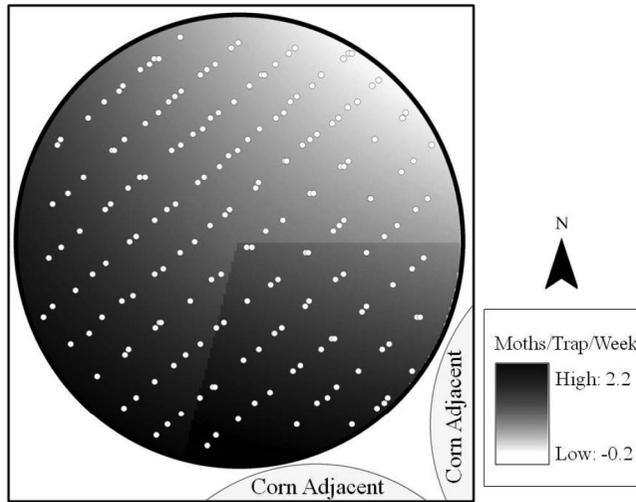


Fig. 1. Modeled average male *O. nubilalis* captured in pheromone traps in a pivot-irrigated corn field calculated before inclusion of the spatial autocorrelation component (i.e., the kriged estimate). Small white circles indicate locations of pheromone traps (Field 2, Wiggins, CO, 1997).

damage from this pest species; Peairs and Capinera 1986). Colorado's irrigated corn is found in a semiarid environment, contrasting with much of the midwestern Corn Belt. In our study region, as distance increases from irrigation, the availability of quality action sites for *O. nubilalis* likely decreases, making irrigated corn more attractive than grassy regions outside of the crop (Lee 1988, Hunt et al. 2001).

Our model estimated the coefficient for the prevailing wind variable as expected if males do not immediately leave the corn field to search for action sites. That is, more moths were found in traps located on the upwind side of the field.

This result is interesting because it suggests that mating may not be entirely random, violating one of the key premises of the high-dose refuge strategy. That is, in regions where females select action sites within

corn fields, possibly because of a lack of moisture or quality action sites external to the field (e.g., SE Alberta; Lee 1988), males emerging within field may not leave the field, and thus, avoid the refuge.

Combining the three directional components (NS, EW, and their interaction term), our model indicated that more moths were trapped in southwestern portions of the field sites. The southwestern portion of the field should accumulate more heat than other regions of the field because of the insolation effect, resulting in decreased moisture with increased temperature (e.g., Chapin et al. 2002). Temperature and moisture components are important factors for development, mating, and oviposition (Webster and Carde 1982, Royer and McNeil 1993, Mason et al. 1996) and may have a noticeable effect on moth behavior, especially if viewed in aggregate over the course of a season.

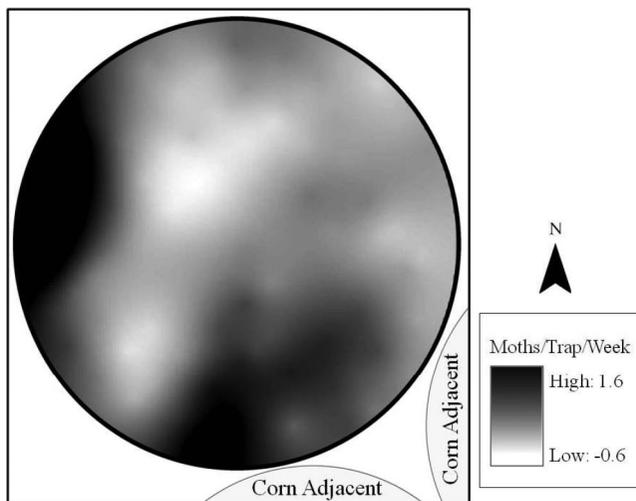


Fig. 2. Model-averaged kriged interpolated surface depicting moth density per trap (Field 2, Wiggins, CO, 1997).

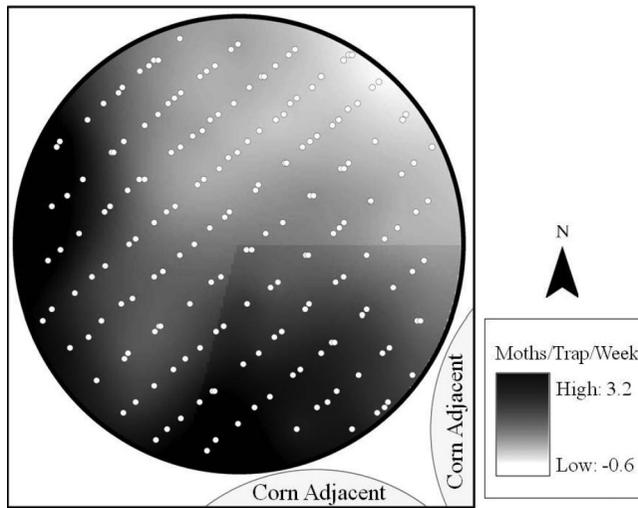


Fig. 3. Final modeled average male *O. nubilalis* moths captured in pheromone traps in a pivot-irrigated corn field. Small white circles indicate locations of pheromone traps (Field 2, Wiggins, CO, 1997).

Conversely, Kira et al. (1969) found that fecundity and fertility decreased without continuous access to moisture, which should suggest that regions with high insolation would be less inviting than within-field locations with less insolation and more available moisture.

A positive edge effect was found, which supports previous spatial lepidopteran research findings (Bailey et al. 2007, Merrill et al. 2011). Specifically, more moths were captured on field edges, suggesting that a portion of male moth population originated outside of the corn field site. This contrasts with findings of Lee (1988), who found increasing moths toward the center of pivot-irrigated corn in Alberta. However, Lee's (1988) pheromone placement design differed substantially from ours. For example, during one sample year, the outermost (closest to the edge) pheromone trap was 150 m within the field. Moreover, in the region tested by Lee (1988), the center of the pivot was the most humid zone.

The elevation variable, which was used as a rough proxy for plant height, had the weakest explanatory value of the variables tested. Moreover, elevation was parameterized in the opposite direction from that indicated by the literature (Mason et al. 1996, Sappington 2005). Although previous findings have shown that high points are attractive as mating sites (e.g., Mason et al. 1996), these sites may not be intrinsically attractive to male moths. Alternatively, the elevation scale used during this study (30 m grid of ground level elevation) may not accurately map elevation at plant height or map to the scale of plant height to which moths respond. For example, moths may respond to high individual plants as contrasted with higher portions of the field, or moths may select the most phenologically advanced fields (as suggested by Sappington 2005). In this study, elevational differences were slight (the maximum within-field elevational difference was ≈ 7 m at each site). Consistent effects may

be observable with larger within-field differences. Moreover, higher elevations (within field) are more exposed to wind, and thus drier, which may have a negative effect on moths in water-limited locations (Kira et al. 1969).

Our findings suggest that a portion of the captured male moths likely originated from outside of the tested field sites. Specifically, the edge effect and the corn adjacent effect (Sappington 2005) suggest moth populations originating externally, or alternatively, leaving the field before reentering the field to search for mates. However, the direction of the prevailing wind direction effect suggests that a portion of the male moth population originated from within the corn field. That is, if moths started their searching behavior from outside the fields, then followed pheromone plumes into the field, trap catches would be expected to be greater on the downwind side of corn fields, which was not supported by these data.

Moths appear to be aggregating using a signal in addition to those signals tested or at alternative scales to those tested. For example, moths may cue on microclimatic factors, such as relative humidity or available drinking water (Kira et al. 1969, Webster and Carde 1982). Moreover, as previously noted, moths may be attracted to elevational points with the corn field at different scales than were tested (e.g., the individual plant scale).

Nevertheless, adjusted R^2 values support the argument that the variables tested are picking up a strong signal in male moth distributions. This work provides more information about dispersal and spatial behavior of *O. nubilalis* with implications for *Bt* resistance management. For example, these findings have refuge strategy implications by suggesting that moth populations both from inside and outside of the field are being attracted to within-field pheromone traps. Our data supports research that suggests moth movement is likely between adjacent fields, further, that adjacent

crops planted to susceptible (non-Bt crops) will act as refuge crops using a high-dose refuge strategy in this semiarid region (Hunt et al. 2001, Showers et al. 2001, Bailey et al. 2007). However, the direction of the prevailing wind effect suggests that many males are searching within-field for mates, arguing that mating may not be entirely random. If sterile insect releases were considered, our findings suggest that a within-field release point is not mandated for males searching for sexually active females because the edge effect and adjacent corn field effects suggest that a large portion of the male moth population appears to be actively searching at a scale larger than the field scale. Further studies should address whether these findings can be extended to regions with different precipitation regimes (e.g., corn-producing regions with more action sites external to the corn field). Additional study should seek to clarify the proportion of male moths that do not leave the field when searching for females, and thus, quantify the degree of nonrandom mating in populations in semiarid regions. These results provide insight into pest ecology, should aid in refining pest management tactics and provide direction for further examination of the high-dose refuge strategy assumptions.

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