Almond moth oviposition patterns in continuous layers of peanuts

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ARTICLE INFO

ABSTRACT

The spatial distribution of eggs laid over a 48-h period by individual female almond moths, Cadra cautella Walker (Lepidoptera: Pyralidae), was examined in bioassays where peanuts covered either the center quarter (quarter-coverage) or the whole (whole-coverage) of a 120-cm square arena gridded into 3 by 3-cm cells. The mean total of eggs laid in quarter-coverage bioassays was not significantly different from the mean in whole-coverage bioassays, i. e., neither food coverage limited oviposition. However, the maximum count of eggs laid in any cell was higher in whole- than in quarter-coverage bioassays, and eggs were more aggregated near edges of the arena in whole-coverage bioassays than near edges of the peanuts in quarter-coverage bioassays. In addition, eggs were aggregated near the release point where females initially encountered food cues. These results suggest that almond moth oviposition behavior in continuous areas of peanuts was similar to patterns observed previously for stored-product insect oviposition in small, scattered food patches. In both cases, females walked or flew between separate oviposition events where eggs were laid in small clumps or lines. Possible behaviors resulting in aggregations of eggs near edges of food, walls, boundaries, or entrances are discussed and implications for precision targeting of insects in food storage areas are considered.

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1. Introduction

Almond moths, Cadra cautella Walker (Lepidoptera: Pyralidae), are important pests of stored peanuts worldwide (Prevett, 1964; Champ, 1966; Freeman, 1974; Hagstrum and Stanley, 1979). Almond moth larvae have lower dispersal capacity than adults and usually complete their development near where they eclosed (Hagstrum and Subramanyam, 2010). Consequently, the behavior patterns employed by females to find and oviposit in food patches have profound impacts on offspring survival.

Several authors have investigated oviposition patterns of stored product moths in food patches of different sizes and food quality. Arbogast and Mullen (1978) found that a closely related species, Plodia interpunctella (Hübner), oviposited nonrandomly in 9-cm-diam. dishes of rearing medium over a 1-week period in a 9 m^2 arena maintained in total darkness. They hypothesized that females

alighted at random on dishes and then laid clumps of 6–60 eggs before taking flight again. This behavior would result in females expending their entire complement of eggs in relatively few dishes. Nansen et al. (2006) examined oviposition by P. interpunctella females in 5- and 10-cm-diam. dishes of wheat kernels and found that they distributed their eggs in proportion to surface area. Similarly, Hagstrum (1984) found that when patches with different numbers of peanuts were present in an experimental warehouse, female almond moths distributed their eggs among patches in proportion to the numbers (i. e., surface area) of peanuts in the patches. Not laying all their eggs at one location was advantageous; however, females laid an excess of eggs at all food densities. This suggests that the females were able to locate and assess quality of fragmented food patches using chemosensory, visual, and tactile cues but, once landing on a patch, they did not allocate eggs in a way that precisely matched the quantity of food available.

Several statistical methods have been developed to characterize patterns of distribution of biological quantities such as counts of individuals or eggs. The ratio of variance to mean, for example, has been used widely by ecologists to distinguish aggregated distribution patterns from random or uniform distribution patterns

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(Southwood, 1978; Perry et al., 2002). This approach has been reviewed and refined further by others, including Haase (1995) and Hurlbert (1990). Two commonly used assessments of distribution pattern include an index of aggregation, I_{M2}, introduced by Morisita (1959), and an index of departure from randomness, D_p, introduced by Hurlbert (1990). Relationships among counts at different locations can be assessed by variogram analysis (Liebhold et al., 1993) and Spatial Analysis by Distance Indices, SADIE (Perry, 1998; Perry and Dixon, 2002).

Our objective in this report was to investigate the spatial distribution of eggs laid by individual almond moths in environments where food is widespread in continuous layers rather than scattered in small patches. Such environments simulate visual, chemosensory, and tactile cues encountered in completely stocked storage rooms and warehouses. Egg-count means and variances were measured and spatial distribution analyses were conducted to examine oviposition patterns when individual females were released into a 120-cm-square arena in which peanuts covered either the center quarter or the entire floor. We hypothesized that almond moth females oviposit in continuous layers of peanuts similarly to the way other stored product insects previously were observed to oviposit in small, scattered food patches (e. g., Arbogast and Mullen, 1978; Campbell and Hagstrum, 2002; Hagstrum, 1984; Nansen et al., 2006). Several previous studies of Lepidopteran searching behavior patterns have found that adults frequently are found in aggregations at the edges of food patches because they usually turn and follow edges of the patches before feeding, ovipositing, or emigrating (see e.g., Campbell and Hagstrum, 2002; Nansen et al., 2004; Haynes and Cronin, 2006). If oviposition behavior is similar in continuous layer of peanuts to that observed previously in small, scattered food patches, aggregations of eggs might be expected to occur wherever females first encounter peanuts, either 1) near where they first entered the arena at the beginning of the bioassay, or 2) near walls where they had been resting (e.g., Hagstrum and Davis, 1980; Nansen et al., 2004), or 3) near the perimeter of the peanut layer when they had been flying in the uncovered part of the arena.

2. Materials and methods

2.1. Insects and bioassay arena

Adult almond moths recently collected from a peanut warehouse were reared at 14:10 L:D photoperiod, 27 °C (±3 °C), and 60% RH (±5%) on a standard diet consisting of ground dog food, rolled oats, white cornmeal, whole wheat flour, wheat germ, brewer's yeast, glycerol, and honey (Silhacek and Miller, 1972). Almond moth pupae were sexed, isolated as male–female pairs, and upon eclosion, individual mating pairs of adults were released from a 25-ml vial into the center of a 120 by 120-cm wooden arena with a 30-cm-height Plexiglas cover. The arena floor was divided into a 40 by 40 grid of 1600 3-cm-square cells. The position of each cell in the arena was designated in vector (x, y) coordinates as the number of cells along each axis from an origin set at one corner. In-shell, Virginia-cultivar peanuts covered the entire arena (23 replications) or only the center quarter (24 replications). The peanuts were obtained from a warehouse and were cleaned of debris before use. New peanuts and new male–female pairs were used for each replicate. The arena was maintained at 14:10 L:D photoperiod under ceiling-mounted fluorescent lights in a laboratory conditioned at 25 °C and 50% RH. The numbers of eggs in each cell were counted 48 h after the mating pairs were placed into the arena, as observations indicated this was sufficient time for several oviposition events to have occurred at different locations in the arena.

2.2. Comparisons of effects of food distribution on mean ovipositional responses

Comparisons by t-test (PC-SAS 9.2, Cary NC) were made of the effect of whole- and quarter-coverage of peanuts on means of total oviposition, counts of cells without eggs, and maximum counts of eggs in a single cell. To examine possible edge effects, the average numbers of eggs laid in cells at different positions relative to the arena edges were plotted for each of the two food distributions.

2.3. Effects of food distribution on oviposition randomness and aggregation

The methods used to evaluate egg distribution patterns included two that were selected from a review by Hurlbert (1990) on measurement of spatial distributions of animal populations. Hurlbert (1990) concluded that the mathematical properties of such distributions could be characterized by two statistical features: 1) departure from the Poisson (random) distribution, which could be measured by an index derived in his review, D_p, and 2) the degree of aggregation, which could be measured by the Morisita index (Morisita, 1959), I_{M2}. A spreadsheet function (POISSON.DIST in Microsoft Excel) was used to estimate random distributions of counts of eggs per cell (egg density, ρ) for comparisons with measured distributions.

The D_p index was applied to measure overlap between the observed distribution of eggs among cells and the random, Poisson distribution. This index varies from 0 to 1, with 0 indicating perfect agreement with the Poisson distribution. A value approaching 1 would occur if almost all eggs were oviposited into a single cell.

The I_{M2} index was applied to compare the observed probability of two eggs being laid in the same cell against the probability that they would be laid in the same cell if the female oviposited randomly (Hurlbert, 1990). An $I_{M2} = 1.0$ occurs when the probability is equal to that from random distribution of eggs among cells. If $I_{M2} < 1.0$, then the observed eggs are less clumped than those of a randomly distributed population (uniform distribution), and $I_{M2} > 1.0$ indicates that the observed eggs are more aggregated than those of a randomly distributed population. For example, $I_{M2} = 4$ means that the probability of finding two eggs in one cell is four times greater than would be expected if the distribution of eggs was random.

2.4. Effects of food distribution on oviposition spatial structure

The spatial structure of egg distributions was evaluated by (omnidirectional) variogram analysis (Liebhold et al., 1993) and SADIE (Perry, 1998; Perry and Dixon, 2002). Variogram analysis (Liebhold et al., 1993) relates the variance of a stochastic process to lag distance, D. In this experiment, the stochastic process is the number of eggs per cell, ρ, and the lag distance between specific pairs of egg-containing cells is the Euclidean distance between them. The lag distance between adjacent cells is $D = 0$. The variogram analysis generates values for three parameters: *nugget*, *sill*, and *range*. The *nugget* parameter represents the variance at $D = 0$ and is therefore an estimate of the stochasticity or unexplained variance in the spatial structure of the distribution. The *sill* estimates the traditional sample variance, and the difference between *sill* and *nugget*, i. e., the *partial sill*, is the amount of variance explained by the spatial analysis. The *range* parameter is the maximum D at which cell observations are spatially correlated.

In this study, the three variogram parameters were generated by fitting a commonly used exponential model (Liebhold and Sharov, 1998):

$$V(D) = nugget \times sill(1 - \exp(-3 \times D/range)) \quad (1)$$

where $V(D)$ is the variance at the specified lag distance, D. Liebhold et al. (1993) recommended that variogram analysis should be based on data within half the shortest length of the sampling universe. Thus, with the arena being divided into a 40 by 40 grid of cells, the combination of lag distance and lag intervals should not exceed half the width of the arena, i. e., 20. Consequently, variogram analysis (PROC VARIOGRAM in PC-SAS 9.2 (Gary, NC, USA)) was performed with the following settings: lag distance = 2, maxlags = 10. For statistical analysis of *sill* and *range*, 1 and 40 were used as maximum values, respectively. It should be noted that the units of *nugget* and *sill* parameters are (egg counts per cell)^2 and the *range* is specified in units of 3-cm cells although, for convenience of interpretation, *range* is converted to units of cm in much of the text.

The SADIE computer software to analyze spatial arrangements is described in Perry (1998), and the free software can be downloaded at http://home.cogeco.ca/~sadiespatial/index.html. The SADIE analysis computes an index of aggregation, I_a, by measuring the minimum distance, D_m, required to move all eggs to complete uniformity (Perry et al., 1999). The degree of randomness is quantified by comparing the observed D_m with the mean value obtained from rearrangements in which the counted eggs are randomly redistributed among the 1600 cells during 1000 permutations. The index of aggregation, I_a, is the ratio of the observed D_m to the mean value obtained from these permutations. The spatial distribution is considered significantly aggregated if the observed value of D_m is greater than in 950 of the 1000 random permutations ($P < 0.05$).

3. Results

3.1. General characteristics of oviposition in whole- and quarter-coverage bioassays

A total of 4738 eggs were laid by 23 females in the whole-coverage bioassays (2.96 eggs per cell, 0.129 per cell per female), and 5105 eggs were laid by 24 females in the quarter-coverage bioassays (3.19 eggs per cell, 0.133 per cell per female). Peanut distribution did not significantly affect the total oviposition by almond moth females or the number of cells without eggs (Table 1). With peanuts covering the whole arena, 94% of cells had fewer than 5 eggs (36,593 of 36,795 total cells sampled), and 99% of eggs were laid in cells with fewer than 10 eggs. Similarly, with peanuts covering the center quarter of the arena, 95% of cells had fewer than 5 eggs (37,722 of 38,022) and 99% of eggs were laid in cells with fewer than 10 eggs. However, the mean of the maximum number of eggs per cell was larger in whole-coverage (11) than in quarter-coverage bioassays (8) (Table 1).

The highest levels of oviposition per cell per female occurred in two of three regions of the arena, depending on the peanut distribution: 1) near the center, where the females initially entered the arena and found peanuts, 2) along the edge of the arena when peanuts covered the whole arena, and 3) near the perimeter of the peanuts when they covered only the center quarter (Fig. 1). In the whole-coverage bioassays, for example, three of 23 females laid a total of 25 eggs 18-20 cells from the arena edge, near where they were released in the center of the arena, resulting in a peak of 0.29–0.36 eggs per cell per female in this region. In the quarter-coverage bioassays, three of 24 females laid a total of 15 eggs near the center, resulting in a peak of 0.07–0.18 eggs per cell per female. In whole-coverage bioassays, eggs were laid on the peanuts in many cells of the first four rows of the arena, resulting in a peak of 0.11–0.29 eggs per cell per female in this outer region. The quarter-coverage bioassays had peak values of 0.3–0.55 eggs per cell per female near the perimeter of the peanuts. The large Standard Errors near the center of the arena (20 cells from arena edge) were due to counts of eggs in a small number of cells being averaged at the center (4 cells averaged per female) compared to the increasingly larger numbers of cells averaged for positions at the edge of the peanuts (76) and the perimeter (156).

On multiple occasions almond moth females flew to rest on walls or top of arena after an oviposition event. At other times, individuals often were seen resting on the Plexiglas top and wooden sides of the arena. Such occurrences were not quantified for this report, but occurrences of females resting on walls have been noted and quantified previously in Hagstrum and Davis (1980).

To place the overall distribution of eggs in the context of a random or a completely uniform distribution, the distributions observed in the whole- and quarter-coverage treatments are shown in Fig. 2 along with the Poisson and uniform distributions expected from averaging both treatments. The Poisson distribution (dotted line in the figure) was calculated using a mean $\rho = 3.08$ eggs per cell, based on the mean total number of eggs laid in the 1600 cells in the two treatments. The Poisson distribution closely follows the two treatment distributions in the interval between 3 and 8 eggs per cell but, outside this interval, it takes on values lower than actually observed. The estimated ρ for a uniform distribution is marked with an asterisk at $\rho = 3.08$ and frequency = 1600.

3.2. Randomness, aggregation, and variogram analyses

For all replications of both whole- and quarter-coverage treatments, the departure from randomness index, D_p, exceeded the value of 0 expected from a random distribution, ranging overall from 0.04 to 0.13. The Morisita aggregation index, I_{M2}, varied from 7.4 to 113.5, exceeding the value of 1.0 expected from a random distribution and also exceeding the values <1 expected for a uniform distribution. However, although they indicated significant departures from randomness, the mean values of the D_p and I_{M2} indices for whole- and quarter-coverage bioassays were not significantly different from each other (Table 2). In contrast, SADIE analysis revealed significant differences between whole- and quarter coverage, indicating that eggs were more aggregated when the distribution of peanuts was whole- rather than quarter-coverage, with I_a ranging from 2.207 to 4.4215 in whole-coverage, and from 1.312 to 2.938 in quarter-coverage bioassays.

When peanuts covered only the center quarter of the arena, the estimate *range* values for all but three of 24 females were within the 40-cell (120 cm) perimeter of the arena. However, only eight of 23 females in the whole-coverage bioassays had estimated values of *range* < 120 cm, due to the clumping of eggs near the edges, increasing the distances over which the egg counts were spatially correlated. Because values of *range* > 120 cm were not biologically meaningful in this experiment except as an indication that the distribution of eggs was spatially correlated through the entire arena, the variogram parameters of the other 15 whole-coverage-
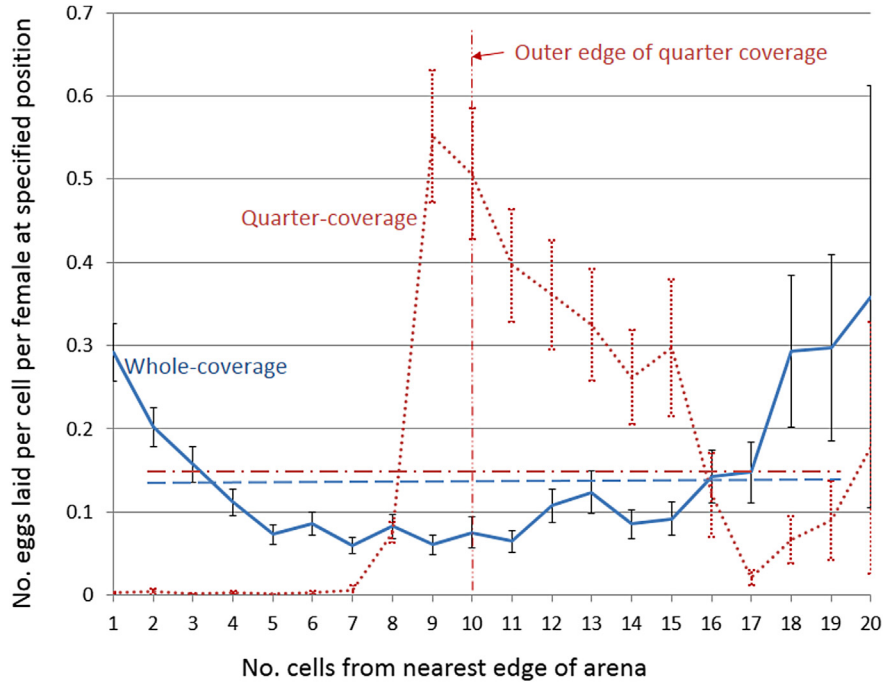
Table 1
Effect of peanut coverage treatment on almond moth oviposition in arena cells.

| Measurement	Peanut coverage (mean ± standard error)		t^a	P
	Whole[b]	Quarter[c]		
No. eggs per female	206.0 ± 41.6	212.7 ± 47.8	−0.51	0.61
No. cells without eggs	1504 ± 31.9	1508 ± 32.5	−0.47	0.64
Maximum No. eggs per cell	11.0 ± 4.5	7.7 ± 4.3	2.55	0.01

[a] df = 45.
[b] n = 23.
[c] n = 24.

Fig. 1. Mean ± Standard Error of numbers of eggs laid per cell per female at specified cell distances from nearest edge of the bioassay arena (solid line and error bars for whole-coverage, and dotted line and error bars for quarter-coverage bioassays). For context, the graph also displays the mean overall rates of eggs laid per cell per female (whole-coverage, dashed line; quarter-coverage, dash-dotted line) and the outer edge of food in the quarter-coverage bioassay (dash-dot-dotted line).

bioassay females were not included in this analysis. In bioassays with *range* < 120 cm, peanut distribution significantly influenced only the *sill* (Table 3), the (maximum) variance that occurs between points that are far enough apart for the egg distribution to be spatially independent.

To examine the variety of different spatial patterns of oviposition observed in the bioassays, examples of egg distribution maps of females whose variograms had minimum and maximum *range* or *partial sill* values are shown in Fig. 3. For both whole- and quarter-coverage peanut distributions, the minimum of *range*

occurred when eggs were laid in small numbers of widely scattered clumps, each with large numbers of eggs, as for female W13, which had a *range* of 5.65 (17 cm), a *partial sill* of 0.13, and a *sill* of 0.33. Female W13 also had the minimum *partial sill* value of the whole-coverage bioassays. A large *range*, as with female W6, generally indicated that eggs were widely distributed. Female W6 had a *range* of 117 cm, a *partial sill* of 0.14, and a *sill* of 0.34. Female Q16 had the maximum *range* in quarter-coverage bioassays, 75 cm, with a *partial sill* of 0.62 and a *sill* of 0.80. Female Q20 had the minimum
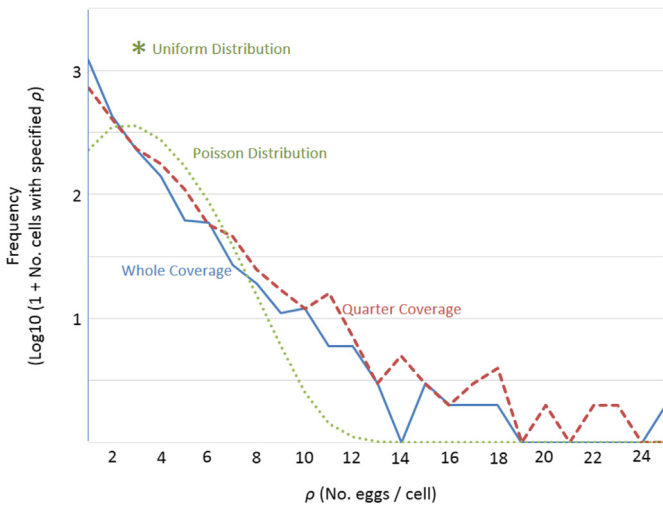
Fig. 2. Effect of whole (solid line) or quarter (dashed line) coverage of peanuts on frequency of occurrence of cells containing specified numbers of eggs per cell in the 1600-cell arena. Expected Poisson distribution is shown in dotted line, and uniform distribution is marked as asterisk. Vertical scale was logarithmically transformed as log10 (1 + No. cells).

Table 2
Effect of peanut coverage treatment on spatial indices of egg counts.

| Index	Peanut coverage (mean ± standard error)		t^{a}	P
	Whole[b]	Quarter[c]		
Departure from Poisson, D_p	0.08 ± 0.02	0.09 ± 0.02	−1.81	0.08
Morisita, I_{M2}	25.0 ± 15.3	27.9 ± 24.1	−0.51	0.61
SADIE aggregation, I_a	3.0 ± 0.7	2.3 ± 0.4	4.22	<0.001

[a] df = 45.
[b] n = 23.
[c] n = 24.

Table 3
Effect of peanut coverage treatment on variogram parameters.

Parameter	Peanut coverage (mean ± standard error)		t^{a}	P
	Whole[b]	Quarter[c]		
Nugget	0.28 ± 0.11	0.27 ± 0.11	0.15	0.88
Sill	0.22 ± 0.07	0.60 ± 0.22	−7.30	<0.001
Range	20.2 ± 12.8	15.2 ± 4.8	1.08	0.31

[a] df = 27.
[b] n = 8.
[c] n = 21.
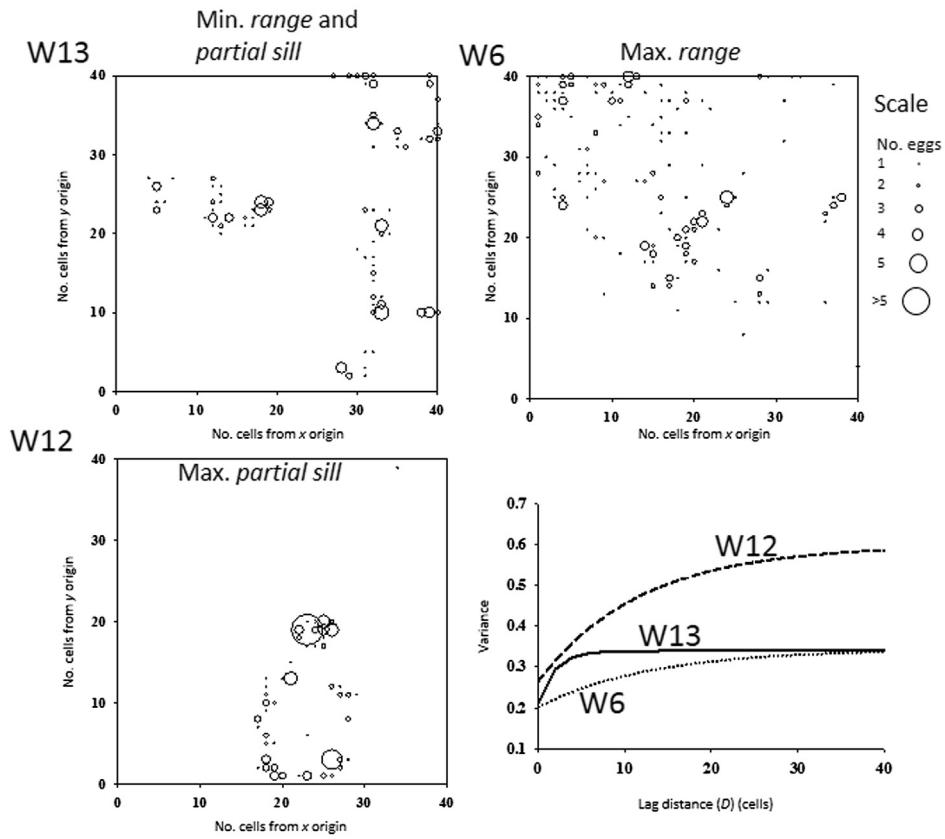
A) Whole-coverage bioassays
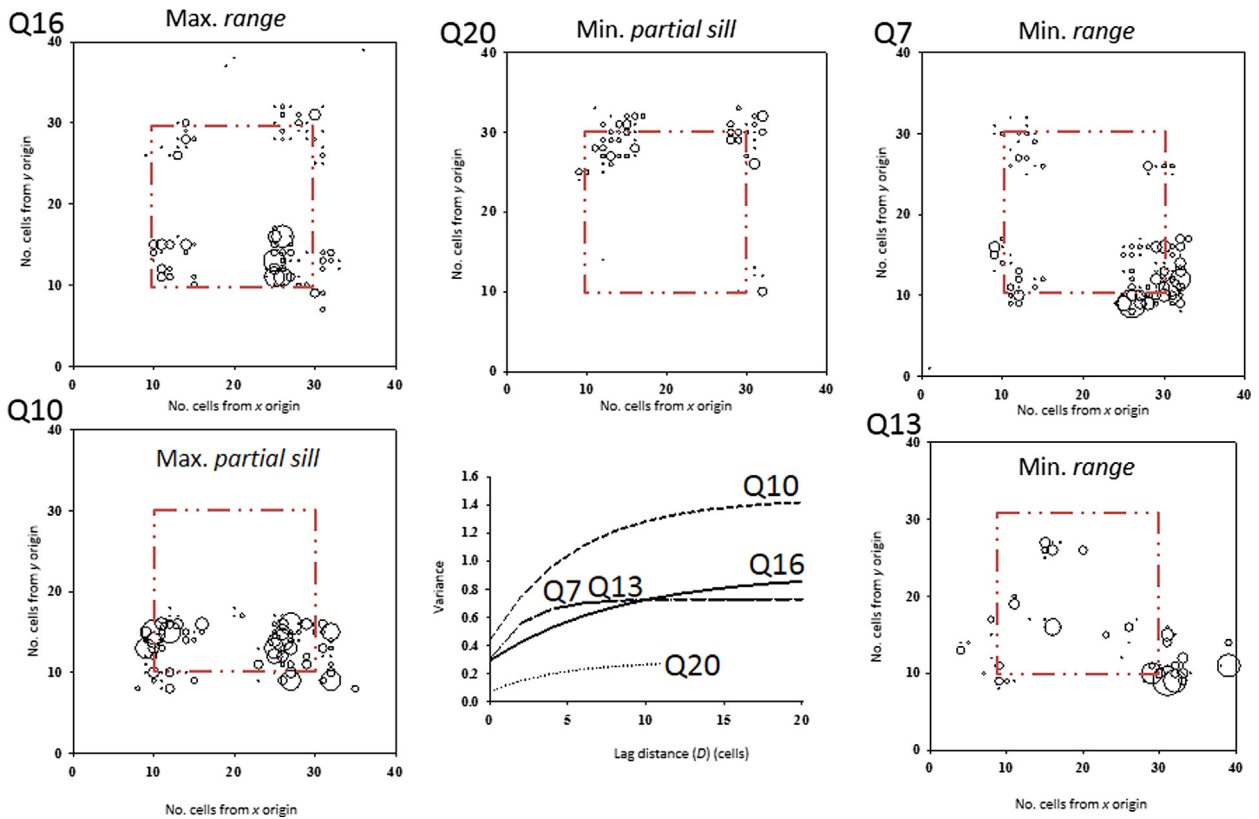
Fig. 3. Examples of egg distribution and variogram plots of females with maximum or minimum *range* or *sill* parameter values in A) whole-coverage bioassays or B) quarter-coverage bioassays. Outer edge of food in quarter-coverage bioassays is indicated by dash-dot-dotted line.

partial sill of those in quarter-coverage bioassays, 0.16, with a *sill* of 0.21 and a *range* of 41 cm.

Maximum values for *partial sill* in whole- and quarter-coverage bioassays were found for female W12 and female Q10, 0.33 and 1.0, respectively. Female W12 had a *range* of 106 cm and a *sill* of 0.6. Female Q10 had a *range* of 49 cm and a *sill* of 1.42.

With only the center quarter of the arena covered with peanuts, distributions were observed where females oviposited near 2 corners of the peanut cover (Q10), 3 corners (Q13) or 4 corners (Q7, Q16 and Q20). Females Q7 and Q13 had identical variogram parameters (minimum *range* of 20 cm, *partial sill* of 0.30, and *sill* of 0.62) but very different egg distribution maps. Greater numbers of eggs were laid near corners than midway between corners, but the differences were not statistically significant.

4. Discussion

4.1. Oviposition patterns

The oviposition patterns of female almond moths in a warehouse with patches of residual peanuts were simulated in a previous study by Hagstrum (1984). It was observed that females distributed eggs among different patches in proportion to the spatial area covered with food. This study extends the simulation context further to oviposition patterns in a stocked warehouse where food is widespread in continuous layers. Here, the levels of oviposition were greatest 1) near where the females initially entered the arena and found peanuts, 2) along the edge of the arena when peanuts covered the whole arena, or 3) near the edge of food when peanuts covered only the center quarter of the arena (Fig. 1). The distributions in Fig. 2 are consistent with a hypothesis that females walked or flew between oviposition events where they laid clumps or lines of eggs nonrandomly, with some cells in a clump occasionally containing more than eight eggs. This pattern is similar to what Arbogast and Mullen (1978) observed with *P. interpunctella* ovipositing in small dishes of peanuts, which suggests that stored product moths may have retained the original adaptations of their antecedents for oviposition in environments with scarce, small food patches. In such an environment, reproduction might be constrained by more by the time available for locating suitable oviposition sites than by the number of eggs available for oviposition (Refsnider and Janzen, 2010). Although Arbogast and Mullen (1978) did not find increased numbers of eggs near the arena edges as was observed in this study, possibly because the experiment was conducted in darkness, large numbers of egg were found in dishes near where the females were released in the center of the arena.

4.2. Egg aggregations at edges

The occurrences of egg aggregations at food and arena edges that were found in this study bear similarity to occurrences of aggregations of adults (Nansen et al., 2005; Haynes and Cronin, 2006), larvae (Nansen et al., 2004), and eggs (Campbell and Hagstrum, 2002) of other insect species near perimeters where adults avoided crossing or could not cross an edge, but were not repelled by the edge. In this study, aggregation of eggs was greater near the edge of the arena in whole-coverage bioassays than was found near the edge of peanuts in quarter-coverage bioassays. This suggests that the combination of a physical perimeter with the edge of a food layer resulted in greater egg aggregation than resulted from females encountering only a food patch edge. It is possible that differences in the levels of aggregation were affected by differences in the proximity of the food to sites where females could rest prior to oviposition.

In addition to the differences in levels of aggregation observed between whole- and quarter-coverage, there were also differences in the capability of the variogram analyses to estimate *range*, the maximum distance of spatial correlation, in the two treatments. Covering only the center quarter of the arena with peanuts provided a buffer zone between the peanuts and the outside edge of the arena in which there were no peanuts and little oviposition. As suggested by Haase (1995), a buffer zone can correct variograms for edge effects. Without the buffer zone, most females oviposited near the edge of the arena and *range* could not be estimated because the egg distributions were spatially correlated throughout the arena. With the buffer zone, *range* values for all but three of the females could be estimated. Also, the higher mean value for *partial sill* with peanuts covering only the central quarter of the arena suggests that, with the buffer zone, more of the total spatial variance is explained by the variograms than without the buffer zone.

Three of the examples in Fig. 3 Q7, Q13, and W13, are of particular interest in this study because the females apparently moved far enough between oviposition events that there was no correlation between the eggs laid at distant locations within the peanut layer. In this context, the values of *range* (<21 cm) may have been estimating the spatial extent of individual egg aggregations rather than the spatial correlations extending around the arena or peanut layer perimeters. As noted by Ettema and Wardle (2002), *range* is dependent on the scale of the aggregations (clumps), i. e., it depends on both the numbers of individuals in the clumps and the distances between clumps. Both small and large values for *range* could occur with the same treatment, depending on whether individual females moved small or large distances between separate oviposition events where small or large numbers of eggs were laid. In general, the occurrence of large numbers of small clumps results in smaller *range* values and the occurrence of small numbers of large clumps results in larger *range* values.

4.3. Inferences about oviposition in commercial storage facilities

Populations of stored product insects monitored with pheromone traps in commercial storage facilities often have foci of increased trap captures within distances of 1–5 m near areas of preferred food (e. g., Arbogast et al., 2002; Arthur et al., 2013). The results of this study indicate that female almond moths are likely to oviposit clumps of eggs near where they first encounter such food sites or near where they have alighted to rest before ovipositing. The relative importance of host substrate volatiles (Campbell and Runnion, 2003; Nansen et al., 2006; Allmann et al., 2013), walls, patch edges, and other visual features (Quartey and Coaker, 1992; Campbell and Runnion, 2003), as well as the effects of predators and intraspecific competition on oviposition behavior (e.g., Tasin et al., 2011; Renwick and Chew, 1994) remain to be clarified for almond moth as well as many other stored product insects. Nevertheless, when designing management programs to precisely target infestations, we can apply knowledge that is already known about how different food odors and visual cues influence where insects aggregate and oviposit in food storage areas.

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