



Almond moth oviposition patterns in continuous layers of peanuts

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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 (Prevelt, 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 m² 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 ($\pm 5\%$) 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):

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