Ovipositional Stimuli of Angoumois Grain Moth (Lepidoptera: Gelechiidae), a Primary Pest of Stored Grains[1]

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Abstract Ovipositional preferences of *Sitotroga cerealella* (Olivier) were measured in the laboratory to characterize the stimuli eliciting oviposition in this widespread pest of stored grains. Substrates used for oviposition included grains presenting both physical and chemical stimuli as well as surrogates presenting only physical stimuli. Chemical factors associated with grains stimulated oviposition, but physical stimuli, primarily the presence of crevices, were of much greater importance. Moths reared for approximately 15 generations in the laboratory were less sensitive to grain factors than were moths more recently collected from the field. Experiments with surrogrates presenting a precisely defined range of crevice sizes confirmed that ovipositional response increased as crevice size narrowed. The results suggest that factors influencing habitat selection are probably very important in this insect because of indiscriminate oviposition on substrates that present appropriate physical stimuli but are entirely unsuitable for larval consumption.

Key Words *Sitotroga cerealella,* Angoumois grain moth, oviposition, stored products.

Angoumois grain moth, *Sitotroga cerealella* (Olivier), is a widely distributed primary colonizer of stored grains. As such, it is able to infest intact grains, causing not only direct damage by larval feeding but also indirect damage by increasing susceptibility of grain to infestation by secondary insect colonizers and fungi. Infestation occurs in the field prior to harvest or in storage. Most reports concerning ovipositional stimuli of this insect have been published with a view to increasing egg production for provisioning parasitoids. Ellington (1930) reported that eggs are readily laid in folded construction paper, and Mills (1965) and Peters (1971) suggested refinements to this method for increasing egg production. Stockel (1969) and Zlotin et al. (1976) reported that the presence of corn kernels and aqueous corn extract, respectively, increased oviposition by *S. cerealella* but no systematic studies have been conducted to document the relative importance of various stimuli eliciting oviposition by this important pest of stored grains. The objectives of this study were to: (1) document the role of physical (shape) and chemical stimuli on oviposition by *S. cerealella;* and (2) examine in detail the relationship between crevice size and oviposition.

Materials and Methods

Insects. Two populations of *S. cerealella* were tested, one that had been in laboratory culture for 2 to 3 years (approximately 12 to 18 generations) (designated "lab"),

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and one that had been in laboratory culture for only 3 generations (designated "field"). Insects were reared on corn ('DeKalb 689') in 0.9-l canning jars housed in a growth chamber at 27 ± 1°C under a 12:12 (L:D) light regime, and 50 ± 11% relative humidity.

Ovipositional bioassay. All experiments were conducted in growth chambers at our standard rearing conditions. Ovipositional assays were conducted in 0.9-l canning jars laid on their sides and containing 20 to 25 adults of mixed ages and sexes. Ovipositional stimuli were presented in Petri dishes (3.5 cm diam × 1.0 cm). Typically, two treatments were compared at a time. The two dishes containing ovipositional substrates were separated by a third dish containing moistened cotton which served as a source of drinking water. Assays were conducted for 2 to 3 days, with at least 6 replicates conducted for each comparison. The treatments were arranged as a randomized complete blocks, with each replicate (jar) considered as a block for each comparison.

Organic substrates. Corn ('DeKalb 689') was used as the standard ovipositional treatment. Corn was grown at the Kentucky State University Agricultural Research Farm, Franklin Co, KY, and maintained at 12 to 13% moisture content. For all assays involving corn, only kernels with flattened sides (from interior sections of the ear) were used, except for the kernel shape test, where flattened kernels were compared to rounded kernels from the tip of the ear. Because the germ side of a corn kernel from the interior of the ear is typically concave and the opposite side is nearly flat, a choice test was conducted to compare ovipositional acceptance of kernels placed germ side down versus germ side up. The glume was removed from all kernels prior to testing. Soybeans ('Fayette', 12% moisture content) were used to compare shape differences within organic substrates. For all assays, the number of corn kernels or soybeans placed in an ovipositional dish was fixed at 6 and 12, respectively, as this was the maximum number that could fit in a single layer in the bottom of the dishes.

Inorganic substrates. River gravel was chosen to test the effect of substrate shape independent of grain-borne chemical stimuli. Pebbles used were similar in size to corn kernels. Spherical glass beads similar in size to soybeans (6 mm diam) were used to complete comparisons of inorganic analogs of corn and soybeans.

Statistical analyses. Data from choice tests with the organic and inorganic substrates were analyzed with analysis of variance (ANOVA) (SAS Institute 1988), transforming data with $\sqrt{x + ½}$ when necessary to homogenize variances, and are presented here as percentages of eggs laid to facilitate comparisons between experiments.

Surrogates. In order to systematically test the effect of crevice size on oviposition, a series of 4 surrogates was fashioned from Polyform® modeling compound (Polyform Products, Schiller Park, IL). The surrogates (1 cm diam × 0.5 cm) had flat tops and convex bottoms, the degree of convexity differing among the 4 surrogate sizes. The gap between the convex surface of a surrogate and the flat surface of the substrate created a crevice, the size of which depended on the degree of convexity of the surrogate. Surrogate #1 was hemispherical, with an outer crevice "height" of 0.5 cm (radius of curvature = 0.5 cm) (Fig. 1). The radius of curvature for the remaining surrogates was chosen so that the crevice height was successively halved between adjacent surrogate sizes, ending with a height of 0.0625 cm for #4. After shaping, surrogates were baked for 20 min at 135°C to harden.

Ovipositional acceptance of surrogates was measured with a four-choice test, placing a Petri dish of each surrogate size (six surrogates per dish) and a dish of moistened cotton in standard ovipositional jars. Surrogates were washed with soap

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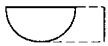
Surrogate		Crevice height (cm)	Radius of curvature (cm)
1		0.5	0.5
2		0.25	0.625
3		0.125	1.1
4		0.0625	2.0

Fig. 1. Dimensions and silhouettes of surrogates used for testing the influence of crevice size on oviposition by *S. cerealella.* Radius of curvature is the radius of the spherical surface used to create the mold for forming the surrogates.

and water and allowed to dry before each use. For testing differences in oviposition on the surrogates, numbers of eggs laid were converted to percentages and transformed to arcsine values prior to analysis with ANOVA. The relationship between crevice size and oviposition was analyzed using regression analysis on the percentage of eggs laid.

Results and Discussion

Physical stimuli. Regardless of substrate composition, objects with flat surfaces against the Petri dish bottom were highly favored over other objects (Fig. 2). Surprisingly, lab moths laid similar numbers of eggs under pebbles and corn kernels in a two-choice test (Fig. 2a). Field moths were more sensitive to chemical stimuli than were lab moths, as demonstrated by the shift in ovipositional bias toward organic substrates by field moths in choice tests involving all combinations of corn or soybeans vs pebbles and beads (Fig. 2b). Although the experimental design does not allow for direct testing of differences between the two populations, in each test the percentage of eggs laid was numerically shifted toward the organic treatment for each two-choice test between the authentic grains and the inorganic counterparts. Clearly, however, mechanostimuli provided by crevices had priority over chemical and other stimuli for both populations. Female *S. cerealella* are able to discriminate well among crevice sizes, as evidenced by the fact that they laid more eggs beneath flat-sided corn kernels from the interior of the ear than beneath the more rounded kernels from the tip of the ear (185.0 ± 84.3 vs 61.3 ± 45.9, respectively) ($\bar{x}$ ± S.D.; $F = 40.2$; df = 1,5; $P < 0.01$), and deposited more eggs beneath kernels placed with the germ facing up than beneath those placed with the germ facing down (165.5 ± 79.9 vs 107.0 ± 82.8, respectively) ($\bar{x}$ ± S.D.; $F = 8.61$; df = 1,11; $P < 0.05$). The crevice created by kernels placed with the germ side up is narrower than that created by kernels placed

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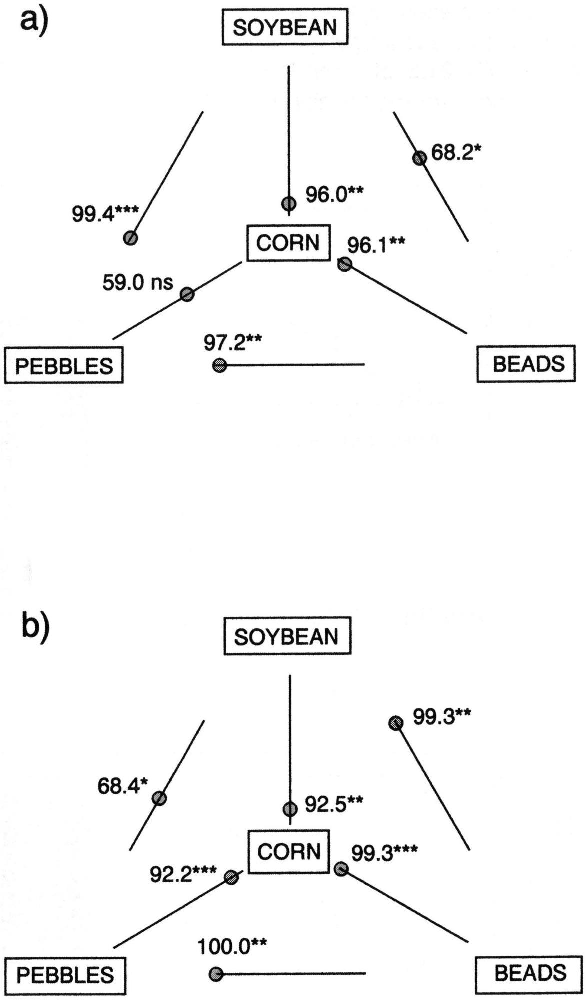

Fig. 2. Oviposition on organic and inorganic substrates in two-choice tests by *S. cerealella* from (a) lab population and (b) field population. Treatments are indicated by boxes, and the position of the circle on the line segment between each pair of treatments represents the degree of bias toward the favored treatment; the number accompanying each circle indicates the percentage of eggs laid on the favored treatment. Asterisks indicate the significance of the difference between the two treatments as determined by ANOVA; *, $P < 0.05$; **, $P < 0.01$; *** $P < 0.001$; ns, not significant.

with the germ facing down because of the concave surface of the germ side and the flat-to-slightly convex shape of the opposite side.

Crevice size. The percentage of eggs laid beneath surrogates increased with decreasing crevice height of surrogates, as expected (Fig. 3). Both populations laid

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most eggs on surrogates presenting the narrowest crevice (#4) and laid successively fewer eggs on surrogates presenting larger crevice sizes. This difference was highly significant for both lab ($F = 21.8$; df = 1,5; $P < 0.0001$) and field ($F = 103.1$; df = 3,12; $P < 0.0001$) populations. The exponential increase in percent oviposition with de-

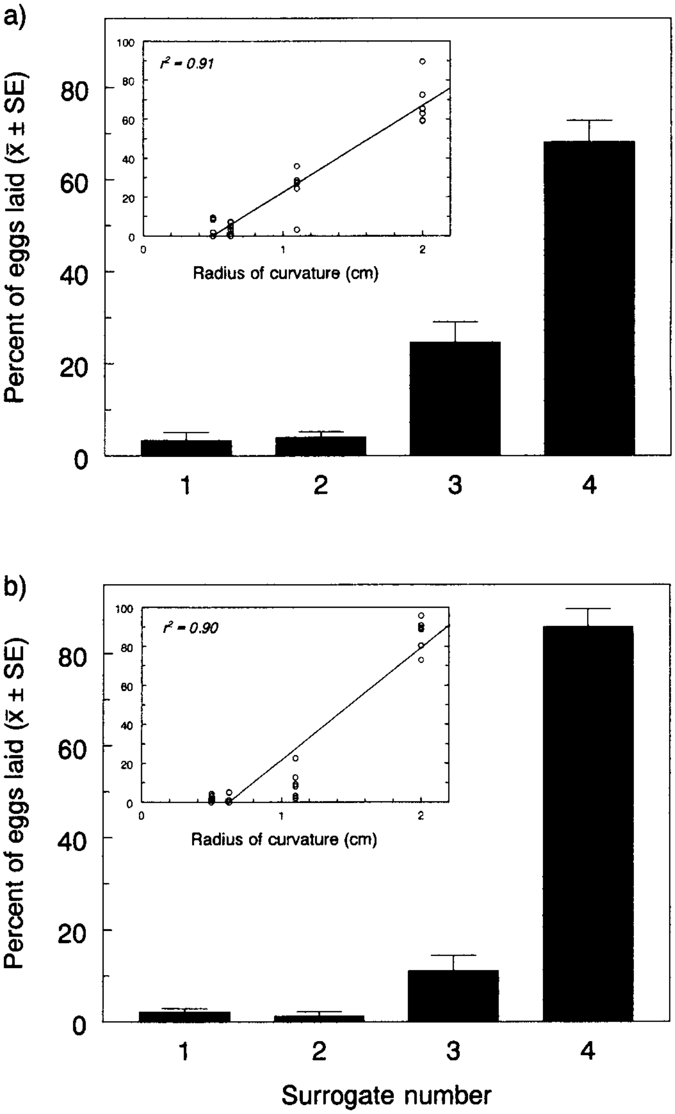

Fig. 3. Relative oviposition on surrogates varying in radius of curvature (crevice height) by *S. cerealella* from (a) lab population and (b) field population. Inset shows linear regression of percentage oviposition versus radius of curvature of the four surrogate sizes.

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creasing crevice height prompted a more detailed analysis of the relationship between surrogate characteristics and ovipositional acceptance.

The critical feature of surrogates perceived by ovipositing females is very likely the surface area of crevices that can be contacted by a probing ovipositor. The surface area of contact is the combined areas of the surrogate and the substrate where the distance between the two surfaces is within a critical range. The relative surface area of crevices of a particular size for surrogates with spherical portions in contact with the substrate is directly proportional to the radius of curvature of the surrogate. [PROOF: The area of a sphere cut by a plane (a spherical cap) is equal to $2\ \pi rh$, where r = radius of the sphere and h = height of the cap ($h \leq r$). The area of a spherical cap between two heights (h_1 and h_2), in turn, is equal to the difference between the areas of the two caps, $2\ \pi rh_1 - 2\ \pi rh_2$, or $2\ \pi r(h_1 - h_2)$. For sufficiently small values of h relative to r, the projection of this ring on the substrate (the other surface contacted by a probing ovipositor) will be of approximately equal area, resulting in a combined area of contact of $\sim 4\ \pi r(h_1 - h_2)$. Thus, for a given pair of heights, the area of spherical caps of varying radius intersected by this range of heights plus the corresponding area of the substrate below this region is approximately proportional to the radius (r) of the cap.] We found an extremely good fit between radius of curvature of surrogates and percentage oviposition for both lab and field moths (Fig. 3). The regression equation fitted to oviposition data for the lab population was $Y = -22.0 + 44.5X$, where Y = percent oviposition and X = radius of curvature ($r^2 = 0.91$; $F = 234.7$; $P < 0.0001$), and that for the field population was $Y = -35.7 + 57.4X$ ($r^2 = 0.90$; $F = 159.4$; $P < 0.0001$). This supports the idea that surface area of optimally sized crevices predicts relative oviposition among objects that are otherwise identical, and that the optimal crevice size for eliciting oviposition by this insect is no larger than that presented by the surrogate with the smallest crevice height (0.0625 cm). We suspect that the optimal crevice height is likely to be close to the diameter of the ovipositor, which is approximately 0.025 cm (P.A.W., unpubl. data).

Confinement to laboratory rearing conditions apparently resulted in decreased sensitivity to chemical factors associated with grains, judging from the greater response toward the authentic grain treatments in two-choice tests among females of the field population relative to the laboratory population (Fig. 2). Slight changes in response to mechanostimuli were also observed (Fig. 3), but the extent of this change was not nearly as large as the change in responsiveness to chemostimuli. This change in behavioral responsiveness occurred rather quickly (i.e., within 2 to 3 years or about 15 generations), and emphasizes the need to periodically introduce field-collected individuals into insect colonies maintained in the laboratory, or to regularly collect insects from the field and establish populations more representative of feral individuals. Including both laboratory and field strains in bioassays can be very instructive for understanding plasticity of both behavioral and physiological traits of insects.

Although surface components of corn kernels stimulate oviposition, the fact that inorganic substrates completely unsuitable for larval development are readily accepted for oviposition suggests that habitat selection is probably critical in this insect. Factors influencing orientation to suitable substrates (i.e., grains) at long range are probably important for *S. cerealella,* but at present are undocumented. It is known that adult males are preferentially caught in pheromone traps located in plots of maturing corn versus adjacent open fields (Stockel 1971, Barney and Weston 1994), and that physical characteristics of corn and other cues, probably volatile chemicals, serve to

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localize flight activity of this insect (Weston et al. 1997). It seems likely that similar long-range orientation might occur in response to odors emanating from grain storage structures. The decreased sensitivity of laboratory moths to chemical cues associated with grain might have resulted from decreased selection pressure for this trait; laboratory-reared offspring of females that have lost the ability to respond to chemical cues associated with suitable food sources do not have reduced fitness as they would in the wild.

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