STUDIES ON FACTORS AFFECTING BEHAVIOR, ECOLOGY, AND REPRODUCTIVE SUCCESS OF THE INDIANMEAL MOTH, *PLODIA INTERPUNCTELLA* (HÜBNER) (LEPIDOPTERA: PYRALIDAE)

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CHAPTER I

INTRODUCTION

Grain Storage: A Brief History and Current Statistics

The concept of agriculture and storage of harvested cereal grains started about 10, 000 years ago when humans began storing food in small pits, mud houses, and wooden enclosures (Pimentel 1991, Reed 1992). Modern agricultural technologies, combined with efficient storage systems such as grain silos and large grain bins, transformed the previously subsistence farming prevalent during medieval times to commerce-driven farming at the start of the 19th century. In 2004, world cereal grain production was 2.3 billion metric tonnes and in the United States 389 million metric tonnes of cereal grains were produced (FAO 2004). Post harvest losses of stored grains caused by vertebrate and invertebrate pests in the U. S. can reach 9% of the total grain stored and in the tropical, developing world could reach 20% or more (Pimentel 1991) causing millions of dollars worth economic losses. The major pests that cause damage to cereal grains in storage include vertebrate pests, such as birds and rodents, several species of arthropods, and various fungi.

Damage Caused by Arthropod Pests to Stored Grain

Stored grains and processed food commodities are infested by a wide array of arthropod pests, predominantly insects, which cause both qualitative and quantitative losses (Mason 2003). Immatures and/or adults of several species of insects severely damage stored food causing a significant reduction in food quality resulting in economic losses to the producers (Pimentel 1991). Storage pests reduce the marketability of the bulk grain by lowering the food quality directly through larval and adult feeding, or indirectly by contamination from larval frass, adult body parts, and chemicals secreted by the insects (Mason 2003). Presence of live or dead adults in the inspected stored grain in

the United States will invariably result in lowering of the food grade as mandated by the Federal Grain Inspection Service (FGIS 2004). For example, when 32 or more insect damaged kernels (IDK) occur in a 100 g wheat sample, the FGIS designates the grain as a 'sample' grade, which indicates that the grain is unfit for human consumption, and according to the Food and Drug Administration is 'adulterated' (FDA 1995). The producers incur huge economic losses when their grain is downgraded. In addition to stored grains, milled products are also infested by storage insect pests. Contamination of processed and value-added food products through insect byproducts such as frass, secretions, etc. may cause allergic reactions, disagreeable odor and off-coloration of food (Scott 1991, Olsen et al. 2001), and the presence of insect fragments may lead to rejection of a company's milled product by the consumers and could lead to the company paying hefty penalties to the federal government or settling consumer law suits.

Arthropod Diversity in a Stored Grain Ecosystem

Stored grain ecosystems differ from conventional agro-ecosystems in that the bulk storage areas provide the inhabiting organisms an infinite amount of food and temporal refuge from an unpredictable external environment (Sinha 1995). Consequently, a variety of arthropods infest stored food products and by far the most important group of pests infesting stored grain and value-added food products are insects, and a majority of these insect pests belong to the families Coleoptera (beetles and weevils) and Lepidoptera (moths).

Based on their feeding, stored product insects are classified as either internal feeders, feeding on the inside of the grain, or external feeders, feeding on the surface of grain kernels, on broken kernels, and on processed products such as flour. Internal

feeders include *Sitophilus* weevils (Coleoptera: Curculionidae), stored-product bostrichid "borers" (Coleoptera: Bostrichidae), seed "weevils" (Coleoptera: Bruchidae), and the Angoumois grain moth, *Sitotroga cereallela* (Olivier) (Lepidoptera: Geleichiidae). External feeders include the larger majority of storage pests, such as the flour beetles, carpet beetles, flour and meal moths, and non-insect arthropods such as mites. In addition to arthropods that are primary consumers of grain and grain products, there are other arthropods present in the storage ecosystem that are secondary consumers upon the primary consumers such as predators (e.g. *Xylocoris flavipes* Reuter, Hemiptera: Anthocoridae) and parasitoids (e.g. *Habrobracon hebetor* Say, Hymenoptera: Braconidae). A comprehensive list of arthropods in stored food ecosystems has been reviewed by Hagstrum and Subramanyam (2006). Among the external feeding lepidopteran insects, the Indianmeal moth, *Plodia interpunctella* (Hübner), is perhaps the most common and most important insect pest causing losses to grain and food producers worldwide.

Distribution and Description of *P. interpuntella*

P. interpunctella is distributed throughout tropical Asia, Africa, Europe, and the Americas (Tzanakakis 1959). It was first described by Hübner in 1827 but the name 'Indian meal moth' was coined by Asa Fitch in the United States (Cotton 1963). Currently, two different versions of the same common name for *P. interpunctella*, 'Indianmeal moth' and 'Indian meal moth', are being used in the scientific literature. The Entomological Society of America recommends using the common name 'Indianmeal moth', which will be used hereafter. Adult moths are 10-12 mm long and have a wing span of about 18 mm. Adults are recognized by their wing coloration with the apical half

of the fore wings reddish brown and the basal half with whitish gray scales (Campbell 1962); hind wings being light gray in color. Adults usually rest on the walls or other indoor dark regions and are most active during the night (Richards and Thomson 1932; Silhacek et al. 2003; Madrid and Sinha 1982). The adults are ready to mate shortly after they emerge from the pupa and as soon as their wings dry. After mating, each female lays 150-200 eggs, which are small, oval, and creamy white in color (Brower 1975). *P. interpunctella* eggs are more or less elliptical measuring 0.45 x 0.27 mm with microscopic roughened exterior (Arbogast et al. 1980). Early larval instars are creamy white in color and as the development proceeds, they become whitish yellow with a pinkish tinge (Richards and Thomson 1932; Cotton 1963). There are five instars in the larval period and the final, 5^{th} instar larva measures about 10-13 mm (Hinton 1942; Allotey and Goswami 1990). Larvae cause the most damage by chewing the food and spinning silken webs around the food material during feeding; larvae cause the formation of lumps of food and excreta that, in addition to severely reducing the food quality, may also cause jamming of milling equipment in food processing plants. The fifth instar larvae actively search for suitable pupation sites and thereafter pupate by spinning silken fibers around their body as a protective cocoon. The pupae are light brown in color initially, but turn dark brown and then black just before the eclosion of the adults. Under ideal abiotic and biotic conditions the life cycle of *P. interpunctella*, from egg to adult, is four weeks (Silhacek and Miller 1972; Bell 1975).

Copulation Behavior of *P. interpunctella*

Courtship behavior of *P. interpunctella* was elaborately described by Grant and Brady (1975). Soon after their emergence, the females exhibit a 'calling' behavior

wherein they raise their abdomens and expose their pheromone glands releasing the female sex pheromone. The calling rhythm of female *P. interpunctella* is photoperiod modulated (Nordlund and Brady 1973). Calling is initiated 2 hr into the scotophase and lasts until the start of next photophase. Female *P. interpunctella* produce four sex pheromones, which are (*Z, E*)-9, 12 tetradecadienyl acetate, referred to as ZETA (Brady et al. 1971), (*Z, E*)-9, 12 tetradecadien-1-ol (Sower 1974), (*Z, E*)-9, 12 tetradecadien-1-al (Teal et al. 1995), and *Z*-9 tetradecadienyl acetate (Zhu et al. 1999). ZETA is considered to be the most important pheromone produced by females because it alone can elicit upwind flight and close-range orientation by adult males, although the other pheromones are apparently needed to stimulate the full range of orientation and mating behaviors in males (Zhu et al. 1999).

A male in the vicinity of the female perceives the chemical stimulus, becomes excited and continuously flaps its wings while searching for the calling females. Male 'wing fanning' disperses a close-range male pheromone secreted by scent glands located at the base of the fore wings (Grant and Brady 1975) that brings about female acceptance as indicated by the turning response of the female after becoming stationary (McLaughlin 1982) . After a male finds a female, he touches the female with his antenna and nudges the female. A female that accepts the male raises her abdomen to receive the male genitalia that the male thrusts into the female genitalia during a head-to-head position (Grant and Brady 1975). The male stops wing fanning when copulating and the moths *in copula* turn around with heads pointing in opposite directions and remain in that position for about an hour.

A single male can mate with 6-7 females during its life time and each male transfers a single spermatophore per mating into a female (Brower 1975). Male *P. interpunctella* produce two types of sperm in their ejaculate, unfertile 'apyrene' sperm without genetic material, and fertile, encysted 'eupyrene' sperm (Gage and Cook 1994; Cook and Gage 1995). The numbers of the two types of sperms transferred by a male to a female decrease upon successive matings. However, a reduced ejaculate from a remating male has sufficient 'eupyrene' sperm to fertilize all the eggs in a female and therefore successive matings by males do not have any affect on the fecundity of the female (Brower 1975; Cook 1999). Also, *P. interpunctella* males allocate their sperm depending on the age of the female, with younger females receiving greater number of sperm irrespective of their mating history compared to the older virgin females (Cook and Gage 1995; Cook et al. 1997). Males delayed from mating transfer reduced number of spermatophores to a female resulting in decreased egg production and males that are 5 d old fail to inseminate the females (Huang and Subramanyam 2003). During its life time, a single female on an average can mate with 4 males and can lay a maximum of approximately 450 eggs (Brower 1975).

Host Finding and Oviposition Behavior of *P. interpunctella*

Oviposition is a crucial step for lepidopteran insects as the survivability of an immobile neonate larva depends on the judicious choice of host by the adult female (Renwick 1989) and preference for certain foods is determined by behavioral, genetic, and ecological aspects (Thompson and Pellmyr 1991). A gravid female insect follows a hierarchical pattern of oviposition when a number of potential hosts are available, laying most of her eggs on the most preferred host followed by a less preferred host. Behavioral

sequences leading to oviposition by a gravid female involve searching, orientation, encounter, landing, surface evaluation, and acceptance (Ramaswamy 1988; Renwick and Chew 1994).

Searching and landing behaviors of gravid *P. interpunctella* females are induced by the perception of a food odor or larval contaminated food odors. Wind tunnel studies by Phillips and Strand (1994) showed that gravid females fly upwind in response to a food odor or to a larval contaminated food source but not to larvae alone, and that larval secretions alone can elicit oviposition. Chocolate products containing nuts are very attractive to mated females and elicit an upwind flight behavior and landing on the food (Hoppe 1981; Olsson et al. 2005a). Prior experience of the adult moths in the form of larval feeding or previous exposure of adults to different foods has been shown to affect the orientation behavior of *P. interpunctella* (Olsson et al. 2006). They showed that female moths pre-exposed to a wheat-based diet showed strong upwind flight behavior in a wind tunnel to the same diet regardless of their larval experience on wheat germ diet or chocolate diet.

Although there has been research on the attractiveness of various foods for *P. interpunctella*, only a few studies have been conducted to isolate and identify compounds attractive to *P. interpunctella* females from different foods or combinations of synthetic compounds. Olsson et al. (2005b) identified three compounds in chocolate volatiles, ethyl vanillin, nonanal, and phenylacetaldehyde, which consistently attracted *P. interpunctella* adults. A blend of the above mentioned three compounds was required to elicit an upwind flight and landing on the attractant source by *P. interpunctella* and the landing rate was dependent on the amount of the three-component blend. Uechi et al.

(2007) recently identified 27 compounds from a 3% ether-pentane solution of wheat flour that were attractive to mated *P. interpunctella* females but not to virgin males and virgin females. They found that straight- chained saturated aldehydes (alkanals; $C_6 - C_{10}$) and unsaturated aldehydes (alkenals; $C_7 - C_{11}$) were active components in wheat and nonanal (C_9) was the most important attractant for mated females. Trapping experiments by Toth et al. (2002) showed that more females than males were attracted to a 1:1 mixture of isoamyl alcohol and acetic acid.

Oviposition by *P. interpunctella* females is influenced by physical and chemical stimuli on the host surface. Physical contact with the food is essential for *P. interpunctella* females to accept a food source for laying eggs (Nansen and Phillips 2003) and preventing a female moth from contacting a food source will reduce the number of eggs laid even in presence of host volatiles. After a female moth comes in contact with the food, a net positive effect of all cues on the food surface results in oviposition (Ramaswamy 1988; Renwick and Chew 1994). *P. interpunctella* females lay eggs either singly in the open spaces between the food grains or sometimes in batches of few eggs by sticking eggs on the food particles (personal observation). In a heterogenous environment, gravid *P. interpunctella* females alight randomly on the oviposition sites and lay eggs in batches, which results in an aggregated pattern of egg laying (Arbogast and Mullen 1978).

Ovipositional preference of adult moths is affected by the food type, food quality and quantity, prior experience, presence of conspecifics, and environmental factors such as temperature, relative humidity, and light-dark cycles. As mentioned earlier, it is believed that female insects follow a hierarchical pattern of host selection for oviposition

based on the suitabilities of different hosts for their offspring survival and development (optimal oviposition theory; Jaenike 1978). This is true for wild *P. interpunctella* females, which lay eggs in foods that are good hosts for the survival of their offspring (see Chapter 4). Changes in nutritional quality of food by addition of oils have been shown to enhance oviposition by *P. interpunctella* females. Nansen and Phillips (2003) tested several plant- and animal-derived oils and mineral oils for their effect on oviposition by *P. interpunctella* females. They found that oil-treated wheat kernels received significantly greater numbers of eggs compared to untreated wheat kernels and, of all the oils tested, responses to walnut oil-treated wheat kernels were the strongest. Moreover, some non-food oils such as mineral oil elicited a significantly greater oviposition response from *P. interpunctella* females compared to untreated wheat kernels. In another study, Nansen et al. (2006) showed that walnut-oil treated wheat kernels elicited greater oviposition by *P. interpunctella* females compared to cracked wheat or untreated whole wheat kernels. They found that surface area of the food was an important factor in oviposition, more so than the volume of food or the number of food patches present, and total oviposition by gravid females increased when the number of walnut oil-treated wheat dishes was increased in a test arena.

Prior experience in the form of the females perceiving host volatiles immediately after eclosion influences future oviposition decisions by *P. interpunctella* females. In two choice bioassays, Olsson et al. (2006) showed that female moths pre-exposed to chocolate volatiles preferred to lay eggs in a dish containing chocolate rather than in a dish containing wheat that was their larval food. Conspecific larval-contaminated food elicits greater oviposition compared to food alone or larval contaminated substrate alone

(Phillips and Strand 1994). These authors indicated that stable semiochemicals of low volatility could be involved in eliciting such a response. Lower densities of conspecific larvae or *Ephestia kuehniella* (Zeller) (Lepidoptera: Pyralidae) larvae elicit greater ovipositional responses from *P. interpunctella* females compared to foods infested with higher densities of larvae (Anderson and Löfqvist 1996)

Temperature and relative humidity affect *P.interpunctella* oviposition. Optimal temperatures for *P. interpunctella* egg laying range from 25 to 30°C and relative humidity is an important factor influencing oviposition at higher temperatures (Mbata 1985). *P. interpunctella* oviposition is regulated largely by the light-dark cycles. A gravid female lays most of her eggs during the scotophase, with peak oviposition at the start of the scotophase and gradually decreasing along the dark period (Madrid and Sinha 1982, Bell 1981). The total number of eggs laid by the gravid females and their oviposition rate are influenced by the number of dark periods throughout the female's life time and the light-dark conditions, respectively (Lum and Flaherty 1970). Continuous light inhibits oviposition and an alternating cycle of light and dark period is ideal for oviposition by gravid females.

Immature Development of *P. interpunctella*

Larvae hatch from eggs in 4-7 days depending on the diet and environmental conditions (Mbata and Osuji 1983; Allotey and Goswami 1990). At 15°C and 70% RH, larvae do not hatch from the eggs as all the eggs die due to cold temperature (Bell 1975). However, as the temperature is raised from 20°C to 30°C at 70% RH, the egg hatch period decreases from 6-9 d to 2-4 d. Larvae that emerge from the eggs feed on the available food material and make silken galleries (Richards and Thomson 1932). Larvae

are cannibalistic and feed on conspecific egg shells, unhatched eggs, and dead adult body parts. There are five instars during *P. interpunctella* larval development as determined by the head capsule width (Imura and Sinha 1986; Allotey and Goswami 1990). Male larvae can be distinguished from the females by a dark colored patch on the dorsal side of the larval body that represents the testes as viewed through the translucent cuticle. *P. interpunctella* larvae feed on a wide variety of foods such as cereal grains, legumes, nuts, dried vegetables, flowers, and some spices. The non-feeding, last instar larva searches for suitable sites for pupation and is called the 'wandering stage'. The pupal stage lasts for about a week (Bell 1975).

Development times for *P. interpunctella* differ based on the kind of diet, moisture content of diet, temperature, and relative humidity. LeCato (1976) tested the suitability of 21 different diets for the development of *P. interpunctella.* He found that larvae preferred cracked or broken grains or beans compared to whole seeds. Development times were least and adults were heavier from larvae reared on ground or cracked corn and soybean compared to wheat, rice, peanut, and peas. Similarly, Mbata (1990) recorded lower development times and higher survival of *P. interpunctella* larvae on cracked maize kernels than whole kernels. Allotey and Goswami (1990) found that the mean development period, which was the time from first instar larvae to adult emergence, at 30°C on different food media (groundnut, maize, wheat, and standard rearing medium) ranged from 25.7 d to 46.1 d, with the shortest time for development on standard rearing medium and then on broken sorghum. Na and Ryoo (2000) tested the suitability of several dried vegetables for *P. interpunctella* larvae and found that development times were shortest on green onions compared to dried carrots, cabbage, and pepper. Johnson

et al. (1992) studied the development of *P. interpunctella* on four different diets (wheat bran, almonds, pistachios, and walnuts) at four different temperatures (25°C, 28.3°C, 31.7°C, and 35°C). They found that, irrespective of the temperatures, *P. interpunctella* development times were shortest on wheat bran which has the highest moisture content (10.3-14%) of the four diets. Regression models based on development times (egg to adult) of *P. interpunctella* from various studies have shown that temperature is the most important factor determining development time followed by relative humidity, and the diet (Subramanyam and Hagstrum 1993).

Population Control Strategies for *P. interpunctella*

Several management practices have been documented in the literature for possible control of *P. interpunctella*. The broad categories of management strategies for *P. interpunctella* populations include 1) physical control, 2) biorational control, 3) biological control, and 4) chemical control.

Physical Control: Human health and environmental risks posed by chemical insecticides have prompted scientists to explore alternative techniques for stored product insect control. Physical control techniques such as proper sanitation, heat and cold treatments, controlled/modified atmospheres, and electromagnetic radiation can be very effective in keeping pest populations low with little or no effect on the quality of stored commodity (Vincent et al. 2003; Heaps 2006).

Insect infestation of stored grains can be reduced by practicing proper sanitary practices. Keeping the farm equipment and empty grain bins free of insects reduces future insect infestation of stored products. Concrete floors are recommended as they are easier to clean (Fields and White 2002). Some other sanitary practices recommended are

plugging holes and cracks, killing insects by impacting grain or flour, and reduce places suitable for insect harbor (Heaps 2006).

Elevated temperatures have been shown to affect the survivorship of different life stages of *P. interpunctella*. One-day old *P. interpunctella* eggs are more tolerant to heat treatments (42-48°C) whereas 3 d old eggs are most tolerant to cold temperatures ranging from 0.5-11.5°C (Lewthwaite et al. 1998). A combination of both hot and cold temperature reduce the time for *P. interpunctella* egg mortality compared to heat alone or cold alone treatments. High temperatures from 46-50°C cause high mortality of both diapausing and non-diapausing larvae (Johnson et al. 2003). Ninety percent of adults die after 70 d of exposure to 10°C (Johnson et al. 1997). Prolonged exposure of adults to 10°C greatly affects the egg production (>50% decrease) and egg viability (90% decrease). Increasing exposure times cause increased mortality of all life stages of *P. interpunctella* between 44-52°C (Mahroof and Subramanyam 2006).

Combination treatments involving controlled atmospheres adversely affect the survival of *P. interpunctella*. Sauer and Shelton (2002) showed that a 12 h exposure of pupae of *P. interpunctella* to a gaseous mixture of 80% carbon dioxide in N_2 at 32.2°C caused 100% mortality. A combination of low pressure (32.5 mm Hg) and high temperature (40°C) causes 99% mortality of eggs, larvae, and adults of *P. interpunctella* in less than 3 h (Mbata and Phillips 2001). Mbata et al. (2004) tested combinations of different temperatures (5-37.5°C) and atmospheric pressures (50 - 300 mm Hg) and found that the time required for 99% egg mortality was lowest at 50 mm Hg and 37.5°C. An initial disinfestation of dried fruits and nuts with low oxygen controlled atmosphere

(0.4% O_2) followed by application of Indianmeal moth granulosis virus (IMMGV) considerably reduces *P. interpunctella* populations (Johnson et al. 2002).

Biorational Control: Female sex-pheromone baited traps are routinely used for early detection and monitoring *P. interpunctella* populations in food facilities (Burkholder 1984; Vick et al. 1986). Sticky pheromone traps usually contain a rubber septum or any other slow release lure that evaporates ZETA, which is a very powerful attractant for males. Several different trap designs are commercially available (Mullen et al. 1997), but the most common type of trap used is the diamond-shaped trap. Pheromone lures can be used for mass-trapping of males (Burkholder 1978), preventing males from finding the females by using high doses of pheromone, referred to as mating disruption (Fadamiro and Baker 2002; Ryne et al. 2001), attract-and-kill strategy, in which an attractant is combined with an insecticide or entomopathogen (Nansen and Phillips 2004), and the 'Push-Pull' strategy, in which pheromone or attractant is used to attract insects to their death, and a deterrent is used to keep the pests away from a space or product (Cox 2004). For *P. interpunctella* females, attractant compounds from different foods are being isolated (Olsson et al. 2005b; Uechi et al. 2007, Nansen et al. U.S Patent Application), however, their efficacy in the field is yet to be confirmed. Another monitoring and detection tool that has been known by pest managers for decades is the black light trap. Different designs of black light traps emitting ultraviolet (UV) light are commercially available (Rees 1985; Harris 2006). Extensive field studies on the effectiveness of black light traps in attracting *P. interpunctella* are lacking, and earlier studies on the attractiveness of UV light to *P. interpunctella* adults revealed contradictory outcomes (Stermer 1959; Soderstrom 1970). Some limitations of currently available

commercial black lights include their large size, high power consumption, non-specificity to insects, and maintenance problems.

Biological Control: Biological control of *P. interpunctella* using pathogens, parasitoids, or predators provides an environmentally safe means of controlling the pest. Probably the most well known pathogen for *P. interpunctella* population control is *Bacillus thuringiensis* Berliner (Bt). The pathogen produces crystal proteins that when ingested by lepidopteran larvae cause pores to form in the midgut, which eventually leads to death of the larvae (Koziel et al. 1993). Although grains from some transgenic crop cultivars expressing toxic proteins affect the development of *P. interpunctella* larvae (Giles et al. 2000), development of resistance to *Bt* toxins is a concern that may affect the future viability of using *Bt* for *P. interpunctella* control (McGaughey and Johnson 1992). The Indianmeal moth granulosis virus (IMMGV) is another microbial pesticide that has shown some promise in controlling populations of *P. interpunctella* especially in stored nuts (Hunter 1970; Vail and Tebbets 1990). Biological control agents such as parasitoids and predators are exempt from registration under USEPA and FDA and they can be freely released in a food facility as long as they don't become food contaminants themselves (Fields and White 2002). The most common parasitoids used for augmentative biological control of *P. interpunctella* include *H. hebetor* and *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae) (Schöller et al. 2006). The warehouse pirate bug, *X. flavipes* is an important predator in the stored grain ecosystem and feeds on eggs, larvae, and pupae of *P. interpunctella* (Donnelly and Phillips 2001), and the larger pirate bug, *Lyctocoris campestris* (F.), another predaceous

Anthocorid, has potential as a bio-control agent for storage pests (Parajulee and Phillips 1992).

Chemical Control: Chemical control of stored product insects has traditionally involved the use of synthetic insecticides. Residual chemical insecticides are applied as surface treatments to empty grain bins, cracks and crevices that can harbor insects in a food warehouse or bin, and as grain protectants and surface dressings to stored grains (Zettler and Redlinger 1984; White and Leesch 1996). Residual insecticides used for 'spot' or surface treatments for empty bins include cyfluthrin, malathion, hydroprene, and diatomaceous earth. Residual grain protectants and surface treatments are among the most common methods of managing insect pests in bulk storages (Arthur 1996). Grain protectants are applied to grain before they are stored. Pirimiphos-methyl, chlorpyriphos-methyl, malathion, pyrethrins, methoprene, diatomaceous earth are some of the most commonly used grain protectants in the food industry (White and Leesch 1996). Insect resistance has been a problem with grain protectants, especially malathion (Zettler 1982; Arthur et al. 1988). Upper layers of grain can also be treated with an insecticide if it is not possible to treat the whole grain; this is called surface dressing or top dressing. Chlorpyriphos-methyl, pirimiphos-methyl, malathion, methoprene, and *Bt* can be used for surface dressing of grain (White and Leesch 1996).

Fumigation is a process of treating the atmosphere in a stored product environment with a toxic gas so that all pest life stages are killed. The most prominent fumigant used for killing insects in post harvest commodities, food processing facilities, food shipments, and soil is methyl bromide. Methyl bromide is a rapid acting and broad spectrum pesticide that kills insects in less than 48 hr in space fumigations (Fields and

White 2002). Despite its advantages, methyl bromide is an ozone depleter and has been banned from use in the United States and other developed countries under the Montreal Protocol starting 1 January 2005, except for quarantine purposes (Anonymous 2000). Phosphine gas, hydrogen phosphide, is a commonly used grain fumigant and potential alternative to methyl bromide, but resistance to phosphine has been discovered in some places (Chaudhry 1997; Zettler et al. 1989). Other problems with phosphine include slow rate of action, it is corrosive to metals, especially copper, and its flammability above certain concentration in air (Bond et al. 1984; Arthur and Phillips 2002; Thoms and Phillips 2004). Phosphine residues on stored grains are minimal and non-toxic, and therefore other improvements are being made to improve the efficacy of phosphine, e.g. addition of CO_2 (Ren et al. 1994), to mitigate insect resistance to phosphine. Currently, sulfuryl fluoride and carbonyl sulfide are being studied as alternative fumigants for their effectiveness in controlling several stored product insect pests.

Rationale and Justification

P. interpunctella is an important insect pest of stored grains and milled food products. Damage is caused by larvae that feed on the stored food resulting in loss of food quality and quantity. Adults moths are short lived (7-9 d) and do not cause any direct damage to stored food. An important but often ignored area of *P. interpunctella* research is the female oviposition behavior. An adult female can mate with five males during its life time and lay an average of 150-200 eggs starting an incipient infestation. Even if a small percentage of the hatched larvae successfully complete their development to adults, a further recurrence of mating among emerged adults and thereafter cyclical generations of *P. interpunctella* would lead to population outbreaks. Understanding the basic biology and behavior of *P. interpunctella* adults is necessary to devise future management strategies that may manipulate adult behavior and avoid use of harmful or environmentally risky chemical insecticides.

After mating, adult females search for suitable oviposition sites to lay their complement of eggs. What factors influence the decision of the females to lay eggs? What is the importance of proximate substrate factors in eliciting an egg laying response by females? Do the female oviposition decisions correspond to their offspring performances on different foods? How does light, with and without semiochemicals, affect behavioral responses of *P. interpunctella*? To answer these questions, laboratory and field studies were conducted for this dissertation to analyze *P. interpunctella* oviposition behavior and study the attraction of adult moths to light and/or semiochemicals.

Research Objectives

The main objectives of this dissertation were to:

1. Study the effects of substrate physical and chemical factors on oviposition by *P. interpunctella* females. Specifically, ovipositional responses of females were studied in response to different textures, numbers, sizes, surface area, and shapes of the substrates applied with chemical stimuli.
2. Investigate whether the ovipositional host preferences of laboratory moths and field- collected moths correspond to their larval performance on eleven different hosts.
3. Study the orientation of adult moths to light, combinations of light and attractants, and ovipositional responses of the females to changes in light duration and scotophase light intensity.

Manuscripts for Publication

Each research objective of this dissertation is elaborated in separate chapters that have been written in the form of manuscripts for publication in peer-reviewed entomology journals. The following is a list of journal papers in preparation from this dissertation:

1. Chapter II. Effect of physical and chemical factors on oviposition by the Indianmeal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) (For publication in: Annals of the Entomological Society of America)

2. Chapter III. Ovipositional preferences and larval performances of two populations of Indianmeal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) (For publication in: Environmental Entomology)
3. Chapter IV. Responses of adult *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) to light and combinations of attractants and light (For publication in: Journal of Insect Behavior)

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CHAPTER II

EFFECT OF PHYSICAL AND CHEMICAL FACTORS ON OVIPOSITION BY THE INDIANMEAL MOTH, *PLODIA INTERPUNCTELLA* (HÜBNER) (LEPIDOPTERA: PYRALIDAE)

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Effect of Physical and Chemical Factors on Oviposition by the Indianmeal Moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae)

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ABSTRACT

Acceptance of a potential host for oviposition by gravid female moths is believed to be predominantly determined by the physical and chemical cues on the substrate surface. We evaluated the effects of substrate physical and chemical stimuli on oviposition by the Indianmeal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae), in a series of laboratory experiments. The experimental arenas were 5.7 liter plastic boxes that contained a single, uncovered 5-cm diameter glass Petri dish with either artificial substrates alone or artificial substrates applied with 0.1 gram-equivalent of a hexane extract of wheat, *Triticum aestivum* L., or 10 g of wheat kernels. Presence of the chemical extract of wheat significantly increased *P. interpunctella* oviposition compared to physical stimuli without extract. A dish surface with spherical glass beads elicited significantly enhanced oviposition compared to surfaces with cheese cloth, filter paper, or sandpaper. Increasing the numbers of similar-sized extract treated glass beads increased oviposition until a certain number of beads was reached, after which the oviposition remained constant. The diameter of the spherical glass beads, rather than the total surface area of beads presented, significantly influenced oviposition, with the 5 mm-diameter glass beads receiving the most eggs. *P. interpunctella* oviposition was also affected by the geometric shape of substrates, with ovoid shapes preferred over cuboid. These studies clearly show that semiochemical and physical cues are required to elicit maximum oviposition by *P. interpunctella*, and suggest that ovipositing females prefer substrates with smooth, round or curved contours.

KEY WORDS physical stimuli, chemical stimuli, chemical ecology, host selection behavior

Host finding by herbivorous insects is a behaviorally complex sequence of events involving host habitat location, host location, and host acceptance (Fenemore 1988, Ramaswamy 1988, Thompson and Pellmyr 1990, Renwick and Chew 1994, Honda 1995). The crucial step of host acceptance by gravid female insects for oviposition is determined mainly by the presence of favorable stimuli on the plant surface (Ramaswamy et al. 1987, Jermy et al. 1988, Renwick and Chew 1994). Ovipositing females perceive cues on the host surface through a variety of sensory receptors like gustatory, olfactory, and mechanical receptors located on different parts of the insect body such as antennae, tarsi, proboscis, labial palpi, and ovipositor (Städler 1974, Städler 1984, Ramaswamy et al. 1987, Hannson 1995). A final decision to oviposit or not is presumably determined by the balance of positive and negative signals perceived by the insect (Renwick and Chew 1994), and an egg laying response can be interpreted as a net positive effect of physico-chemical cues present on the host surface (Dethier et al. 1960, Miller and Strickler 1984, Renwick and Radke 1987, Renwick and Chew 1994).

The Indianmeal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) is a serious and widespread pest of food grains and grain-based products, dried fruits, nuts, and legumes (Cox and Bell 1991). *P. interpunctella* is a common pest in or near food storage areas such as grain bins (Doud and Phillips 2000) and food warehouses (Vick et al. 1986), and commercial settings such as pet food stores, grocery stores (Platt et al. 1998), and restaurants. Economic losses are from the cost of pest control and from the non-marketability of products due to larval feeding and the subsequent silken webs spun by the larvae around the food material.

Management of *P. interpunctella* has traditionally involved the use of fumigants and residual chemical insecticides. However, the problems posed by insecticide usage on finished products have been well documented in the literature (e. g. Arthur and Phillips 2003). Novel pest management strategies involving female *P. interpunctella* sex pheromone, such as mating disruption (Fadamiro and Baker 2002, Ryne et al. 2001, Ryne et al. 2006) and attract-and-kill strategy (Nansen and Phillips 2004), affect only males. Males that circumvent these strategies can mate with 5 or more females, on an average, during their life time (Brower 1975), leading to either persistence or growth of *P. interpunctella* pest populations. Understanding the behavior of female *P. interpunctella* and incorporating such knowledge into management strategies against females could lead to effective pest suppression.

The objectives of this study were to evaluate the oviposition response of *P. interpunctella* to 1) physical stimuli alone or to both physical and chemical stimuli, and 2) to the gross texture, type, number, size, surface area, and shape of potential substrates.

Materials and Methods

Insects. *P. interpunctella* for these experiments were obtained from a laboratory culture of moths that was maintained in a growth chamber at 28°C, 60-70% RH, and 16:8 (L:D) on a standard cornmeal-based diet (Phillips and Strand 1994). Pupae were removed from the laboratory colony, separated by sex, and carefully transferred into 1 x 6 cm shell glass vials and incubated in a growth chamber until they emerged.

Artificial Substrates. Glass beads were used as model systems for studying *P. interpunctella* ovipositional responses to changes in different physical aspects of substrates, because glass beads are chemically inert, easily available, and offer

thigmotactic stimuli similar to natural foods of *P. interpunctella* such as wheat, *Triticum aestivum* L. In experiments involving chemical stimuli, we tried to imitate naturally occurring oviposition sites by addition of 0.1 gram equivalent of hexane extract of wheat to the artificial substrates, and manipulated the glass beads in different ways to study the effect of various physical factors on *P. interpunctella* oviposition.

Wheat Extracts. Extracts of locally grown hard red winter wheat were prepared by weighing and grinding 100 g of wheat kernels into a fine powder using a food blender. The ground wheat was placed in a 500 ml Erlenmeyer flask and extracted for 24 h at 22ºC using 200 ml of hexane (ACS grade, Pharmco Products Inc., Brookfield, CT). The extract was filtered through a filter paper (Fisher Scientific Qualitative 05 paper) into a 250 ml Erlenmeyer flask. The extract was then either concentrated by evaporation under N_2 gas or diluted to 100 ml with additional hexane to prepare a stock solution of 1 gram-equivalent wheat/ml concentration. The stock solution was stored in a 250 ml Wheaton glass bottle (Sigma-Aldrich Corp., St. Louis, MO) at -20ºC in a freezer before being used.

General Bioassay Procedure. No-choice oviposition bioassays were conducted in 5.7 liter (31 x 17 x 11 cm) transparent plastic boxes (Sterilite Inc., San Antonio, TX) with a single 'oviposition dish', which was the bottom of a 5-cm diameter glass Petri dish (50 mm x 10 mm) containing the artificial substrates to be evaluated. The dish was placed either on an uncovered plastic box floor (experiment 1a) or on a plastic box floor with brown craft paper (experiments 1b-6) (Nansen and Phillips 2003). Once initial studies determined the need for chemical stimuli to elicit oviposition by *P. interpunctella*, all artificial substrates in the remaining experiments were treated with a total of 0.1 gram eq. of wheat extract in 200 µL of hexane solution and the control was an empty Petri dish

with 200 μL of 0.1 gram eq. wheat extract applied on its surface. In experiments involving treated glass beads, the extract was applied directly on the glass beads in the Petri dish using a pipette. After the extracts or solvent blanks were applied, the Petri dishes were kept in the fume hood for about 15 min to allow the hexane to evaporate. One pair of 1-2 d old virgin moths was released into the bioassay arena, allowed to mate, and lay eggs for 48 h. All bioassays were conducted in controlled growth chamber conditions at 28°C, 60-70% RH, and 16:8 L:D photoperiod. Eggs laid in the Petri dish, on the floor, and on the walls of the plastic box were counted after the 48 h bioassay period. Used glassware was washed with a detergent in tap water, rinsed with acetone and distilled water, and then oven dried (12 h) before being used for subsequent experiments. Craft paper floor coverings were discarded after counting the eggs. The plastic boxes were cleaned with a detergent in warm tap water, then rinsed with distilled water, and air dried for 24 h before being reused in other bioassays.

Experiments 1a and b. Effect of Substrate Physical and Chemical Stimuli on *P. interpunctella* Oviposition. The objective of experiment 1a was to study the oviposition response of *P. interpunctella* in presence of physical stimuli alone or in combination with chemical stimuli. We used 5 mm diameter glass beads (Fisher Scientific, Pittsburgh, PA) as sources of physical stimuli for *P. interpunctella*. Chemical stimuli were provided by 0.1 gram eq. wheat extract in hexane. No-choice bioassays were conducted with three treatments: 1) untreated glass beads, 2) glass beads with extract, and 3) 10 g wheat kernels as positive control. A total of fifteen replicates were conducted.

In experiment 1b *P. interpunctella* oviposition behavior was observed in response to an empty dish and to different numbers of glass beads when offered without any chemical stimuli; an empty dish with no extract/hexane was control. Thus, treatments were an empty dish, 50, 100, 150, 200, and 250 3-mm diameter glass beads (Fisher Scientific, Pittsburgh, PA). Ten replicates were conducted for each treatment. Since these initial experiments determined that chemical cues were needed to elicit maximum oviposition response by *P. interpunctella* to physical stimuli, all subsequent experiments had hexane extract of wheat applied to substrates and/or to empty dishes.

Experiment 2. Effect of Different Textures of Artificial Substrates on *P. interpunctella* Oviposition. Various substrates were tested for female *P. interpunctella* ovipositional response as follows: 1) 10 g of 3-mm diameter spherical glass beads (approximately 280 beads; Fisher Scientific, Pittsburgh, PA), 2) a 5-cm diameter piece of coarse grade sandpaper (Grit# 60; Norton abrasives, Stephenville, TX), 3) 5-cm diameter filter paper (Whatman #1, Whatman International, UK), and 4) a 5-cm diameter piece of cotton cheese cloth from a local commercial store. Wheat extract (0.1 gram eq.) was applied on the substrates and to the bottom of an empty dish that served as control. Twenty-five replicates were conducted for each treatment.

Experiment 3. Effect of Substrate Number on *P. interpunctella* Oviposition. In no-choice bioassays, 5, 10, 25, 50, 100, 150, 200, 250, 300, and 500 spherical glass beads (3 mm diameter; Fisher Scientific, Pittsburgh, PA) were used to study the ovipositional response of *P. interpunctella* females to increase in the number of substrates in presence of chemical stimuli. The amount of solvent was varied from 100 - 500 µL to account for the increase in the number of beads keeping the total amount of

wheat extract added constant (0.1 gram eq.). Positive control was a dish containing 10 g wheat kernels.

Experiment 4. Effect of Substrate Size on *P. interpunctella* Oviposition. Spherical glass beads measuring 2 mm, 3 mm, 4 mm, 5 mm, and 6 mm (Fisher Scientific, Pittsburgh, PA) in diameter were used in this study. Twenty-five beads were provided in each dish because results from Experiment 3 suggested this to be the minimum number of beads for *P. interpunctella* to direct a greater proportion of her oviposition (>75%) into the dish.

Experiment 5. Effect of Different-Sized Substrates Offering the Same Total Surface Area for *P. interpunctella* Oviposition. In experiment 4, size of the substrate significantly affected the ovipositional response of *P. interpunctella*. To test if this differential response to bead sizes was a factor of total increased surface area of beads as diameter increased, an experiment was designed wherein the total surface area offered by glass beads of each size category was kept nearly constant by adjusting for the number of beads per dish. The numbers of spherical glass beads of different diameters were adjusted so that ca. 28.26 cm^2 of total surface area was presented in each dish. The following diameters and numbers of glass beads (in parenthesis) used were: 2-mm (225), 3 mm (100), 4 mm (56), 5 mm (36), and 6 mm (25).

Experiment 6. Effect of Substrate Shape on *P. interpunctella* Oviposition. Cuboidal, cylindrical, heart-shaped, ovoid, and spherical (~ 7 mm diameter) glass beads (Crafts Etc., Oklahoma City, OK) were used for this experiment. The different-shaped glass beads used for this experiment are typically used for stringing necklaces and bracelets, and therefore each glass bead had a single hole through its middle. The

numbers of beads of each shape used in the experiment, based on their displacement of 1 ml distilled water to approximate similar volumes of space displaced were: cuboidal (6), cylindrical (5), heart-shaped (5), ovoid (15), and spherical (6). Twenty five replications were conducted for each treatment under conditions reported above.

Statistical Analysis. The data were analyzed for 1) the number of eggs in the dish and/or total eggs laid per box and 2) the proportion of total eggs in the dish relative to those deposited in the entire box. Only boxes that had five or more eggs were included in the analyses for calculating the mean proportion of total eggs per dish for each treatment. The five-egg threshold was established because preliminary studies determined that females laying less than five eggs in 48 h were either unmated or otherwise impaired. Raw data for egg counts in Petri dishes and the proportions of total eggs in Petri dishes were transformed using $\sqrt{(X + 0.5)}$ and arcsine square root method (Zar 1999), respectively, to satisfy the assumption of homogeneity of variances for analysis of variance (Little and Hills 1978). The transformed data were analyzed by the PROC MIXED procedure of SAS version 9.1 (SAS Institute 2003). Treatment means were separated by the DIFF option of LSMEANS and tested for significant differences (t-test, $P < 0.05$). Data presented are untransformed means ± standard error of the mean.

Results

Experiments 1a and b. Effect of Physical and Chemical Stimuli on *P. interpunctella* Oviposition.

Presence of chemical stimuli significantly enhanced oviposition by *P. interpunctella* ($F = 5.08$; $df = 2, 42$; $P = 0.0106$). Untreated glass beads offering only physical stimuli received only $1/5^{th}$ the number of eggs that were laid on glass beads treated with 0.1 gram eq. of the wheat extract in hexane (Fig. 1). Proportions

of eggs laid in dishes containing untreated glass beads were significantly lower compared to extract-treated beads or wheat dish ($F = 26.96$; df = 2, 30; $P < 0.0001$). In Experiment 1b no chemical stimuli were present in any treatment and the absence or presence of different numbers of glass beads did not significantly affect the total oviposition per box ($F = 0.35$; df = 5, 54; $P = 0.8798$) or the numbers of eggs laid in dishes by *P. interpunctella* ($F = 0.43$; df = 5, 54; $P = 0.8269$). Very low numbers of eggs were observed across all the treatments (Table 1). The proportions of total eggs deposited in dishes relative to the whole box were statistically insignificant among the treatments ($F = 0.64$; df = 5, 15; $P = 0.6758$).

Experiment 2. Effect of Different Textures of Artificial Substrates on *P. interpunctella* Oviposition. A significantly greater number of eggs were laid when glass beads were provided as artificial substrates compared to other substrates when all substrates were treated with wheat extract ($F = 31.29$; df = 4, 120; $P < 0.0001$). Cheese cloth, filter paper, sandpaper, and an empty dish elicited very low numbers of eggs from female moths. About 9 to 54-fold more eggs were laid on wheat extract-treated glass beads compared to the other substrates (Fig. 2). Significantly greater proportions of total eggs per box were laid on glass beads than in an empty dish, on cheese cloth, or on sandpaper ($F = 36.46$; df = 4, 63; $P < 0.0001$). The lowest proportion of total eggs per box was laid in the Petri dish with filter paper (Fig. 2).

Experiment 3. Effect of Substrate Number on *P. interpunctella* Oviposition. Average total numbers of eggs laid were significantly different across the treatments ($F = 4.43$; df = 11, 288; $P < 0.0001$). Increase in the numbers of glass beads increased the total oviposition by *P. interpunctella* (Table 2). Significant differences were observed in

the numbers of eggs laid in dishes containing different numbers of 3-mm beads and wheat ($F = 7.71$; df = 11, 288; $P < 0.0001$). The numbers of eggs laid increased as the number of glass beads was increased to 150, after which no statistical significance in the number of eggs laid was observed. *P. interpunctella* females laid significantly lower proportions of eggs in Petri dishes that contained 5, 10 or no beads than other treatments ($F = 13.30$; df = 11, 181; $P < 0.0001$). No significant differences in the proportions of total eggs laid per box were observed when 100 or more beads were used (Table 2). Proportion of eggs localized in the dish, which might indicate the presence of optimal substrate stimuli for female moths, increased significantly when 25 glass beads or more were used.

Experiment 4. Effect of Substrate Size on *P. interpunctella* Oviposition. Size of the substrate significantly affected *P. interpunctella* oviposition ($F = 6.29$; df = 5, 144; $P < 0.0001$). A curvilinear ovipositional response was observed as the diameter of the 25 glass beads in each dish increased (Fig. 3). Significantly greater numbers of eggs were laid in dishes containing 4, 5, or 6 mm beads than on glass beads of smaller diameter. The number of eggs laid in dishes containing 25 beads of 5 mm diameter was about 4 times greater than when 2 mm or 3 mm diameter glass beads were used. Significant differences were observed in the proportions of total eggs per box laid in the dish among glass beads of different sizes ($F = 5.64$; df = 5, 89; $P = 0.0001$). Smaller proportions of eggs were laid in dishes containing 2 mm and 3 mm compared dishes containing 5 or 6 mm beads (Fig. 3).

Experiment 5. Effect of Substrate Size Relative to Constant Surface Area on *P. interpunctella* Oviposition. Significant differences were observed in numbers of eggs

laid in dishes when glass beads of different diameters, but offering nearly the same total surface areas, were used ($F = 6.69$; df = 5, 144; $P < 0.0001$). No significant differences in egg counts in dishes were observed when 3-6 mm beads were used (Fig. 4). A 5 fold increase in egg laying was observed when 5 mm beads were used compared to 2 mm beads. Also, significant differences in the proportions of total eggs laid in dishes with different treatments were observed ($F = 17.84$; df = 5, 92; $P < 0.0001$). Significantly lower proportions of total eggs were laid in empty dishes with extract. No significant differences in the mean proportions of total eggs were observed in case of 3-6 mm beads.

Experiment 6. Effect of Substrate Shape on *P. interpunctella* Oviposition. Shape of the substrate significantly affected *P. interpunctella* oviposition ($F = 4.14$; df = 5, 144; $P < 0.0015$). Dishes containing ovoid beads received significantly greater number of eggs (32.8) compared to heart-shaped beads (13.5 eggs). Significantly lower numbers of eggs were laid in empty dishes with no beads (Fig. 5). Mean proportions of total eggs laid in dishes were significantly different among the treatments ($F = 9.28$; df = 5, 75; $P < 0.0001$). Again, significantly lower proportions of eggs were laid in empty dishes without beads (Fig. 5). The greatest proportion of eggs were laid in dishes containing ovoid beads (0.84), however, it was not significantly different from proportions of eggs in dishes containing the other substrate shapes.

Discussion

Results from our experiments clearly show that *P. interpunctella* females require a combination of physical and chemical stimuli for oviposition and that the presence of only chemical or physical stimuli separately is not sufficient for eliciting a maximal oviposition response. A relatively low amount of hexane extract of wheat elicited a

significant increase in the number of eggs laid by females. Extract treated-glass beads provided a close simulation to cereal grains, and we deduce that they offered both thigmotactic and chemical stimuli for *P. interpunctella* females. Other species of moths require both tactile stimuli and chemical stimuli for eliciting an optimal oviposition response. For example, in the spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), oviposition was influenced by both physical and chemical stimuli originating from the host (Städler 1974). *C. fumiferana* females exposed to petroleum-ether washed twigs of balsam fir, *Abies balsamea* (L.) Miller, laid lower numbers of eggs compared to an unwashed host twig. Maher and Thiéry (2004) found that the European grapevine moth, *Lobesia botrana* (Denis and Schiffermüller) (Lepidoptera: Tortricidae) showed a greater oviposition preference for glass beads treated with methanolic/water extracts of grape berries, *Vitis vinifera* L., than untreated glass beads. They concluded that polar compounds in the host extract served as ovipositional stimulants for *L. botrana.* The chemical composition of stimulatory compounds in the wheat extract we used in our studies is not known, but we assume that both non-volatile and volatile components were present in the hexane extract and may have been involved in eliciting oviposition. Further investigation is required before the semiochemical oviposition stimulants for *P. interpunctella* from wheat are known.

P. interpunctella females laid a far greater number of eggs in dishes with glass beads than dishes containing cheese cloth, filter paper, or sandpaper. Moreover, the moths localized their eggs in dishes that contained glass beads, as opposed to being dispersed throughout the bioassay boxes. We conclude that increased egg-laying response was mainly attributed to the direct thigmotactic stimuli provided by glass beads

with chemical stimuli relative to other physical stimuli in Experiment 2, as empty dishes or dishes with cheese cloth, filter paper, or sandpaper, with no or little three-dimensional physical stimuli, elicited the lowest responses from female moths. Similar kinds of behavior have been observed in some species of moths and beetles. The European small ermine moth, *Yponomeuta cagnagellus* Hübner (Lepidoptera: Yponomeutidae), prefers to oviposit on glass substrates resembling host twigs rather than on filter paper (Hora and Roessingh 1999). Similarly, *L. botrana* prefers to oviposit on spherical glass beads resembling grape berries than coarse texture offered by sandpaper (Maher and Thiéry 2004). Städler (1974) found that spruce budworm, *C. fumiferana,* preferred to oviposit on artificial twigs that resemble balsam fir. In the case of beetles, Credland and Wright (1988) found that the cowpea weevil, *Callosobruchus maculates* (F.) (Coleoptera: Bruchidae), laid similar numbers of eggs on untreated cowpeas, *Vigna unguiculata* (L.) Walpers, and glass beads treated with cowpea extract. Rough surfaces offered by filter paper, sandpaper or cheese cloth may have deterred the female *P. interpunctella* from laying eggs in our experiment, as was observed in case of the stem borer, *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae), which was deterred by rough surfaces offered by leaf trichomes on maize, *Zea mays* L. (Kumar 1992). Also, the substrates such as filter paper, sandpaper, or cheese cloth did not offer substantial three dimensional or vertical physical stimuli such as those provided by the natural oviposition sites for *P. interpunctella*, such as cereal grains, nuts or other seeds and fruits. That importance of direct contact with three-dimensional physical stimuli for optimal ovipositional response of *P. interpunctella* is supported by data from Nansen and Phillips (2003), who showed that when *P. interpunctella* females were prevented direct contact with wheat kernels, the females laid

fewer eggs in the food dish despite the volatile olfactory stimuli presumably originating from the wheat kernels.

Our data on *P. interpunctella* oviposition suggests that females make decisions for optimal allocation of eggs based on quality or quantity of the resource patch they may encounter at any given time. Other studies have examined oviposition decisions by stored product insects in response to food patches of varying sizes or quantities. For example, the cowpea weevil, *C. maculatus*, responded to increasing numbers of cowpea seeds by increasing oviposition (Cope and Fox 2003). Campbell and Runnion (2003) showed that oviposition by female red flour beetles, *Tribolium castaneum* (Herbst), reached a peak at a certain patch size of flour media, and that no net gain in fitness occurred when females oviposited in food patches that exceeded the critical patch size. Results by Toews et al. (2000) suggest that the lesser grain borer, *Rhyzopertha dominica* (F.), adjusts oviposition within a patch of seeds related to the total number of seeds in the patch. In our study, *P. interpunctella* oviposition reached a peak at a certain apparent threshold patch size for our artificial system (i.e. bead number) and remained more or less constant thereafter despite increasing patch size. Further research is needed to determine if no additional fitness benefits accrue for progeny of *P. interpunctella* females by laying greater numbers of eggs in large patches that exceed a threshold patch size. Also, other physical or biological constrains of female moths may explain the maximum attained oviposition that we observed.

The size (diameter) of individual glass beads in aggregates, independent of total surface area of the aggregate, clearly influenced the oviposition response of *P. interpunctella* (Experiment 5). Gravid females responded to increased size of glass beads

by increasing their oviposition. Large seeds offer greater amount of larval food for offspring survival in seed-breeding insects than do small seeds. In the case of the bruchid *C. maculatus*, females lay more eggs per seed when supplied with seeds of larger size than when seeds of smaller size are provided (Cope and Fox 2003). The rice weevil, *Sitophilus oryzae* L., prefers larger sized wheat kernels compared to smaller, shriveled ones (Campbell 2002). This preference seems to be justified as the progeny fitness increased when *S. oryzae* oviposited on large size kernels. Although we did not study offspring fitness in the experiments reported here, studies similar to those done with internal seed-feeding beetles (e.g., *C. maculates* and *S. oryzae*), are warranted for *P. interpunctella* in order to study the correlation between oviposition substrate size and offspring fitness.

We found that the shape of potential oviposition substrates had a weak influence on *P. interpunctella* oviposition (Experiment 6). Females laid fewer eggs on substrates that were more flattened relative to the substrate (heart-shaped beads) or that possessed sharp, angular separations of horizontal and vertical surfaces (cube and cylinder-shaped beads) compared to substrates with smoother, more rounded contours (spheres and oval-shaped beads). *P. interpunctella* females seem to prefer substrates that have smooth, curved surfaces. Shape of artificial oviposition substrates, and their similarity to the shape of natural hosts, has been shown to influence oviposition in some insects. The tortricid moth, *L. botrana*, prefers to lay eggs on smooth, spherical fruit models that resemble grape berries, than flat ones (Maher and Thiéry 2004). Similarly, *C. fumiferana*, females prefer to oviposit on needle-shaped artificial models that resemble the host twigs (Städler 1974).

P. interpunctella is a peri-domestic pest of human-produced stored food products, and the "natural" or pre-domestication host plants or oviposition substrates are not known (Linsley 1944, Mohandass et al. 2007). Thus, we can not directly relate the results of our highly controlled laboratory studies to what might be expected from oviposition of *P. interpunctella* on its natural host. Nevertheless, our studies clearly show that *P. interpunctella* females prefer to oviposit on substrates that are similar in size (3-6 mm) and shape (ovoid) to those of seeds from cereal grains and many other pantry species.

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Table 1. Oviposition responses of *P. interpunctella* females to different numbers of 3 mm diameter glass beads lacking chemical stimuli in Experiment 1 b

Treatment	N	Mean (± S.E) egg count per box‡	Mean (± S.E) egg count per dish‡	Mean proportion (± S.E) of total eggs per dish†‡
Empty dish	10	3.8 ± 1.6	0.6 ± 0.6	0.18 ± 0.18 (3)
50	10	24.7 ± 15.9	3.8 ± 2.3	0.17 ± 0.04 (3)
100	10	18.1 ± 16.3	8.3 ± 7.6	0.33 ± 0.08 (3)
150	10	13.0 ± 6.1	3.0 ± 2.0	0.34 ± 0.18 (6)
200	10	10.3 ± 6.2	8.0 ± 5.9	0.61 ± 0.21 (3)
250	10	19.7 ± 11.8	4.2 ± 3.0	0.39 ± 0.28 (3)

† The number of boxes with ≥5 eggs laid per box and used in the calculation of proportion laid in dishes (in parenthesis)
‡ Mean (± S. E) values are not statistically significant ($P > 0.05$)

Table 2. Oviposition responses of *P. interpunctella* females to different numbers of 3 mm diameter glass beads with chemical stimuli provided by 0.1 gram eq. wheat extract in Experiment 2.

Treatment	N	Mean (± S.E) egg count per box[a]	Mean (± S.E) egg count per dish[a]	Mean proportion (± S.E) of total eggs per dish[ab]
Empty dish	25	25.2 ± 8.7de	5.8 ± 2.7e	0.22 ± 0.08d (11)
5	25	16.2 ± 7.3e	1.8 ± 0.6e	0.18 ± 0.07d (11)
10	25	14.0 ± 6.5e	3.5 ± 1.8e	0.19 ± 0.07d (11)
25	25	27.0 ± 8.8de	20.2 ± 7.1cde	0.74 ± 0.09bc (11)
50	25	30.4 ± 8.7cde	16.8 ± 7.2de	0.55 ± 0.10c (16)
100	25	34.8 ± 9.4bcde	30.8 ± 9.0bcd	0.81 ± 0.06ab (19)
150	25	52.8 ± 11.2abc	45.0 ± 10.5ab	0.86 ± 0.05ab (19)
200	25	65.9 ± 13.5ab	57.6 ± 12.8ab	0.84 ± 0.05ab (21)
250	25	61.6 ± 14.0abc	49.1 ± 12.3ab	0.79 ± 0.09b (15)
300	25	75.3 ± 14.1a	59.5 ± 12.3a	0.79 ± 0.07b (22)
500	25	68.7 ± 14.0ab	58.8 ± 12.8a	0.86 ± 0.06ab (20)
Wheat (10 g)	25	42.8 ± 10.8bcd	42.8 ± 10.6abc	0.98 ± 0.01a (17)

[a]Means in a column followed by the same letter are not significantly different (t-test; $P < 0.05$)

[b]The number of boxes with ≥5 eggs laid per box and used in the calculation of proportion laid in dishes (in parenthesis)

Figure Legends

Fig. 1. Oviposition responses of *P. interpunctella* to substrates offering physical stimuli alone or both physical and chemical stimuli. A 'Control' dish contained glass beads treated with hexane only, an 'Extract' dish was a dish containing glass beads applied with 0.1 gram-equivalent wheat extract in 200 μL hexane, and a 'Wheat' dish was a dish containing 10 g wheat kernels. Bars represent mean numbers of eggs per dish and dots represent the proportion of total eggs laid per dish. Bars or dots with the same lower or uppercase letters, respectively, are not significantly different (t-test; $P < 0.05$; N = 15).

Fig. 2. Oviposition of *P. interpunctella* in no-choice bioassays in response to different textures of artificial substrates treated with a hexane extract of wheat. Bars represent number of eggs per dish and dots are the proportions of total eggs per dish that was determined by the ratio of number of eggs laid in dish to the total number of eggs laid in the box. Bars or dots with the same lowercase or uppercase letters, respectively, are not significantly different (t-test; $P < 0.05$; N = 25).

Fig. 3. Oviposition responses of single *P. interpunctella* females to substrates of different sizes in no-choice bioassays. Bars or dots with the same lowercase or uppercase letters, respectively, are not significantly different (t-test; $P < 0.05$; N = 25).

Fig. 4. Mean number of eggs laid by a single *P. interpunctella* female in the dish (bars) and proportion of total eggs laid per dish (black dotted circles) in response to different-sized glass beads offering same total surface area. Means followed by

the same lowercase (bars) or uppercase (dots) letters are not significantly different (t-test; $P < 0.05$; N = 25).

Fig. 5. Mean oviposition responses of single *P. interpunctella* females to substrates of different shapes. Means followed by the same lowercase or uppercase letters are not significantly different (t-test; $P < 0.05$; N = 25).

Fig. 1

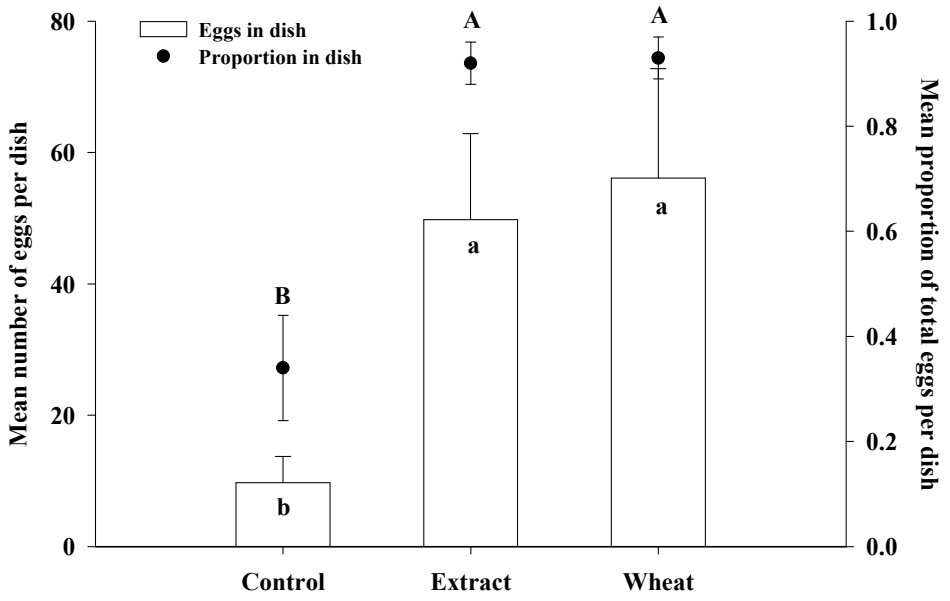

Eggs in dish
Proportion in dish
Mean number of eggs per dish
Mean proportion of total eggs per dish
80
60
40
20
0
1.0
0.8
0.6
0.4
0.2
0.0
A
A
B
a
a
b
Control
Extract
Wheat

Fig. 2

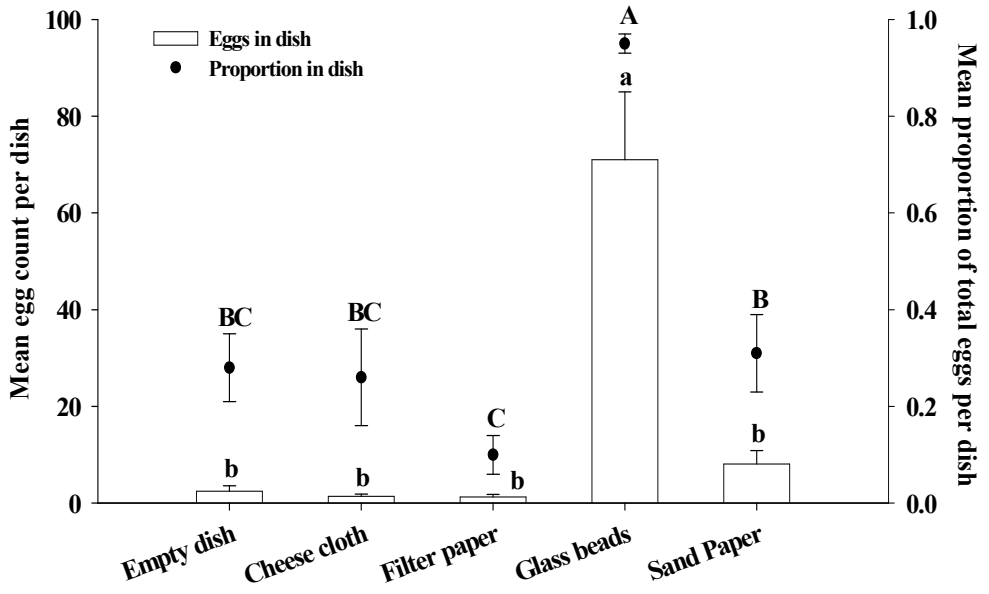

Eggs in dish
Proportion in dish
Mean egg count per dish
Mean proportion of total eggs per dish
100
80
60
40
20
0
1.0
0.8
0.6
0.4
0.2
0.0
BC
BC
C
A
B
a
b
b
b
b
Empty dish
Cheese cloth
Filter paper
Glass beads
Sand Paper

Fig. 3.

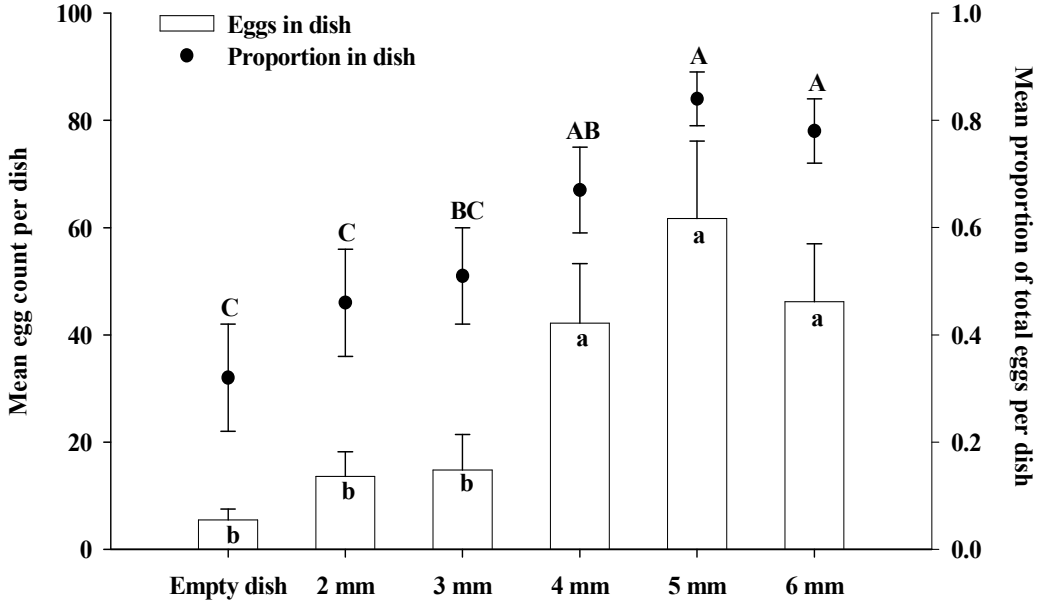

Eggs in dish
Proportion in dish
Mean egg count per dish
Mean proportion of total eggs per dish
100
80
60
40
20
0
1.0
0.8
0.6
0.4
0.2
0.0
C
C
BC
AB
A
A
b
b
b
a
a
a
Empty dish
2 mm
3 mm
4 mm
5 mm
6 mm

Fig. 4.

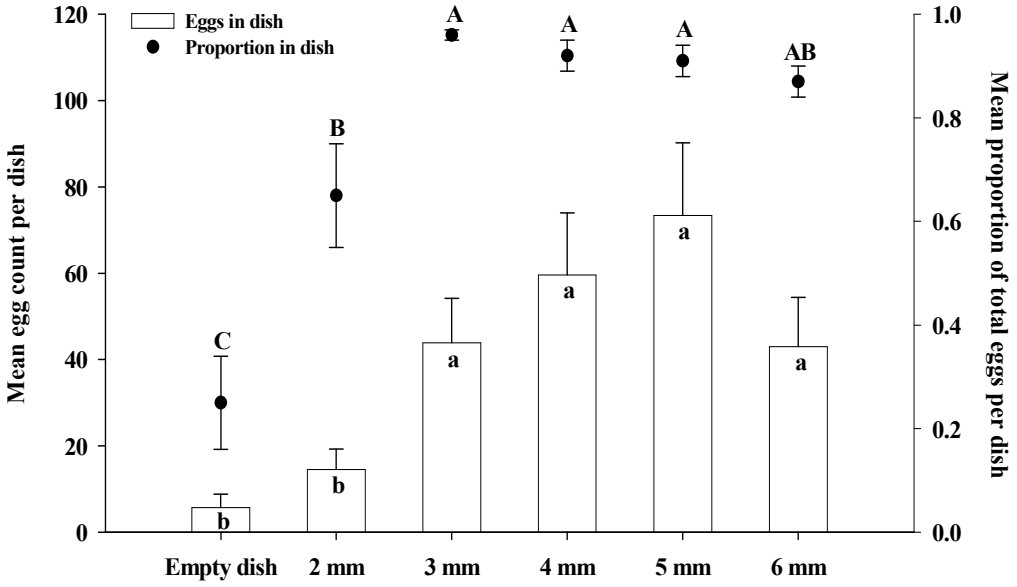
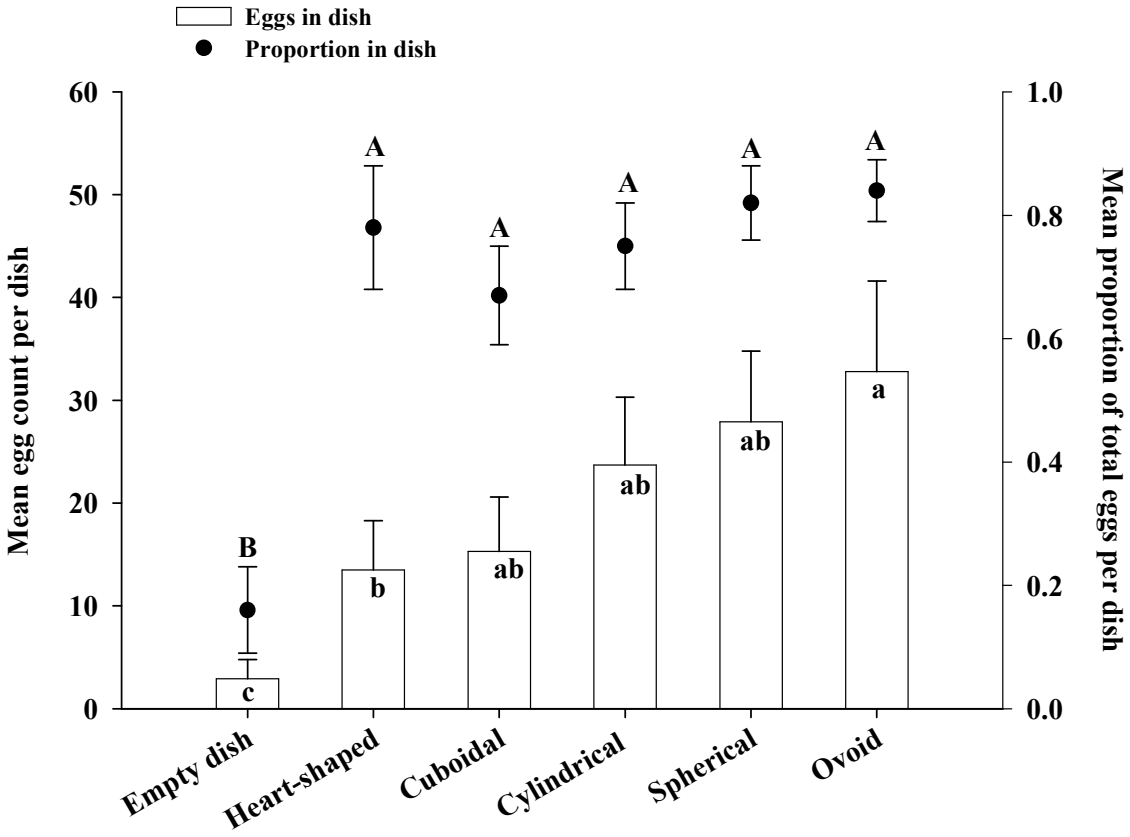

Eggs in dish
Proportion in dish
Mean egg count per dish
Mean proportion of total eggs per dish
120
100
80
60
40
20
0
1.0
0.8
0.6
0.4
0.2
0.0
A
A
A
AB
B
C
a
a
a
a
b
b
Empty dish
2 mm
3 mm
4 mm
5 mm
6 mm

Fig. 5.


Eggs in dish
Proportion in dish
Mean egg count per dish
Mean proportion of total eggs per dish
60
50
40
30
20
10
0
1.0
0.8
0.6
0.4
0.2
0.0
B
A
A
A
A
A
c
b
ab
ab
ab
a
Empty dish
Heart-shaped
Cuboidal
Cylindrical
Spherical
Ovoid

CHAPTER III

OVIPOSITIONAL PREFERENCES AND LARVAL PERFORMANCES OF TWO POPULATIONS OF INDIANMEAL MOTH, *PLODIA INTERPUNCTELLA* (HÜBNER) (LEPIDOPTERA: PYRALIDAE)

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Environmental Entomology

Ovipositional Preferences and Larval Performances of Two Populations of Indianmeal Moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae)

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ABSTRACT

Oviposition decisions by female insects can determine the survivability and fitness of their offspring. In this study, we assessed the larval performance and adult oviposition preferences of two populations of the Indianmeal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae), one a long-term laboratory colony and another recently collected from the field. Development assays on a variety of foods were conducted on individual larvae in small shell vials, and data were collected for survivability (%), development time (d), and adult weight (mg). Larvae from either population did not survive on ground walnut, pecan, coriander, and fennel. There were significant differences in larval survivabilities on lab diet, chick pea, and soybean between the two populations. Development times were longest on prunes and barley. Mean adult weights were highest on chick pea, lab diet, and soybean for the laboratory moths whereas soybean and chick pea were very suitable for the field moths. Overall, field moths weighed significantly less than the laboratory moths. Adult ovipositional preferences were assessed in no-choice and four-choice oviposition bioassays in plastic boxes containing diets differing in quality. In a no-choice situation, laboratory moths laid greater number of eggs on soybean, but the numbers were not significantly different from those laid on apricots and wheat. Field moths laid significantly greater number of eggs on soybean, and those numbers were similar to those laid on barley. In four choice bioassays, laboratory moths were less "choosy" and oviposited in diets previously determined to be unsuitable for their progeny survival. Field moths were more selective and laid significantly greater numbers of eggs on soybean than in dishes containing

barley, coriander, or an empty dish. Our studies clearly show that captive rearing of *P. interpunctella* for long periods can alter the behavioral patterns of immatures and adults.

KEY WORDS Host selection, stored products, adaptation

Oviposition decisions by female lepidopterous insects can be crucial for the survival of their offspring mainly because the neonate larvae of some species are relatively immobile and absence of an immediate, optimal food resource could be detrimental to the development of the larvae and ultimately fitness of the resultant adult will be severely reduced (Thomson and Pellmyr 1991). Indeed, a generally accepted hypothesis for oviposition by a gravid female is that she lays eggs in or on host plants based on their quality and suitability for the insect's offspring, referred to as the optimal oviposition theory or the preference-performance hypothesis (Jaenike 1978). Furthermore, according to this theory, when many hosts are simultaneously offered to a female, it is expected that she will follow a hierarchical order of host preference laying eggs on the best larval diet first, and then on the next best diet, and so forth (Thompson 1988). However, there have been several instances where the post-alightment host preferences of gravid females do not match the developmental performance parameters (e. g. development time, pupal/adult weight, wing length) of the immatures (Gratton and Welter 1998, Foster and Howard 1999, Jallow and Zalucki 2003); and in some cases good correspondence between adult oviposition preferences and progeny survival was observed (Wiklund 1981, Craig et al. 1989, Nylin and Janz 1993, Barker and Maczka 1996, Joachim-Bravo et al. 2001).

An important factor that may determine whether an insect will oviposit or not on a potential host is presence or absence of chemical stimulants and/or deterrents (Jermy 1984, Thompson and Pellmyr 1991, Honda 1995). Presence of optimal concentrations of stimulatory chemicals on the plant surface alone or in combination with physical stimuli such as shape, size, and texture influence the female oviposition decisions (Ramaswamy

et al. 1987, Renwick and Chew 1994; Chapter II of this dissertation). Understanding these insect-host interactions and behavioral mechanisms involved in oviposition responses of female insects to different hosts will provide an insight into the evolutionary patterns of host use and possible host shifts to not-so-favorable hosts when good quality hosts are scarce (Tabashnik 1983, Futuyma et al. 1984).

The Indianmeal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae), infests a wide range of stored food commodities such as cereal grains (Allotey and Goswami 1990, Locatelli and Limonta 1998), legumes (Lecato 1976), dried fruits (Cox 1975), nuts (Mbata and Osuji 1983, Johnson et al. 1995), and some spices (Perez-Mendoza and Aguilera-Penã 2004). Most laboratory research involving *P. interpunctella* or other economically important insect pests are conducted using laboratory cultures of insects reared on artificial food media under constant environmental conditions in order to provide a regular supply of experimental insects. For behavioral studies the laboratory reared insects are assumed to show behaviors that correspond to their conspecific wild counterparts. However, because of continuous rearing for several generations under confined conditions, inbreeding and loss of variability is expected and consequently the laboratory populations may not fully display the behavioral patterns exhibited by the wild populations (Mazomenos et al. et al. 1977, Mason et al. 1987). The possible reasons for this variation in laboratory insects may be due to enhanced effect of deleterious genes caused by continuous inbreeding (Boller 1972, Briscoe et al. 1972, Mackauer 1976, Mukhopadhyay et al. 1997), founders effect (Stuart and Gaugler 1996), no selection pressure for use of different hosts due to the absence of natural enemies (Bernays and Graham 1988), artificial selection for fast development and high productivity, and low

mobility due to confined conditions (Remund et al. 1977). Due to these factors, lab-reared insects may not discriminate among different hosts varying in quality. Compared to lab-reared insects, conspecific insects in the wild are under a high selection pressure for reproductive success in a variable environment that includes the presence of natural enemies, unstable habitats caused by human activity, presence of suitable and unsuitable host plants, rare or dispersed host plants, and varying physical environment (temperature, relative humidity, etc.) conditions. Because the overall individual fitness to withstand these selection pressures in the wild is mainly dependent on the quality of the food resource, it can be presumed that the wild females would be more discriminating during the host selection process than the laboratory insects.

In this study, we separately assessed the performances of progenies from a long-maintained laboratory colony and a recently collected "field" colony of *P. interpunctella* on several different diets. Then, we tested ovipositional preferences of these two populations in no-choice and four-choice bioassays. Specifically, the objectives of this study were to 1) record percent survivorship from first instar larva to adult, development time, and adult weight of progeny from two populations of *P. interpunctella* on eleven potential hosts, and 2) conduct no-choice and four-choice bioassays to evaluate the acceptability and preferences, respectively, of individuals from the lab-reared colony and a field colony for oviposition on a sub-set of the different diets.

Materials and Methods

Laboratory Insects. Our laboratory colony of *P. interpunctella* has been reared on a mixture of cornmeal, chick starter, egg crumbles, and glycerol (4:2:2:1) for 5 years (minimum of~60 generations), with occasional infusion of wild moths, in a growth

chamber at 28°C, 60-70% RH, and 16:8 (L:D) photoperiod. Adult moths of specific age were obtained by placing cardboard rolls in the culture jars for a week to collect the fifth instar larvae and separating the pupae by sex. First instar larvae emerging from the eggs collected from these adults were used for the developmental bioassays.

Field Moths. Wild populations of *P. interpunctella* were collected and combined from several retail food stores in or near Stillwater, OK. Several Styrofoam cups (0.25 L) containing standard lab diet were placed at different locations inside these grocery stores to collect eggs from wild *P. interpunctella* females that would oviposit into them. The cups were replaced weekly and the 1-wk old cups were incubated under controlled environmental conditions, as mentioned earlier. When the wandering stage larvae were observed, the contents of the diet cups were emptied into 0.5 L jars. Adults were separated from the diet jars after their emergence into 0.25 L jars and eggs were collected from several mating pairs. The eggs were then transferred into a 10 cm diameter plastic Petri dish for eclosion, and a small amount of food was added to each dish to retain larvae that might otherwise disperse and escape from the dish. These first instar larvae were used for development studies within 24 h after hatching from the eggs.

Diets. Eleven foods were used for this study including the cornmeal-based lab-rearing diet as the positive control. Seeds or dried fruits from two host plants each from five botanical families were selected as follows: Poaceae: wheat, *Triticum aestivum* L., and pearled barley, *Hordeum vulgare* L.; Leguminosae: soybean, *Glycine max* L., and chick peas, *Cicer arietinum* L.; Juglandaceae: pecan nutmeats, *Carya illinoensis* (Wangenh.) K. Koch, and walnut nutmeats, *Juglans nigra* L.; Rosaceae: apricots without pits, *Prunus armeniaca* L., and plums without pits, *Prunus domestica* L.; Apiaceae:

coriander seeds, *Coriandrum sativum* L., and fennel seeds, *Foeniculum vulgare* Miller. These foods were either USDA certified organic products (Sun Organic Farms, San Marcos, CA) or had no additives as per the manufacturer's specifications. Moisture contents of these diets were determined by adding 2 g of a diet to a 5 cm diameter glass Petri dish and oven drying the sample at 80°C for 48 h. Three replicates were set up per diet. Dishes containing dried foods were transferred to a chamber containing a desiccant (Alumina adsorption, Fisher Scientific, Fair Lawn, NJ) to prevent the food materials from absorbing atmospheric moisture after their removal from the oven. Dry weights of the foods were determined and percent moisture contents were calculated, which were: wheat-10.9%, barley-10.4%, soybean-9.9%, chick pea-8.9%, pecan-7%, walnut-4.7%, apricots-33.5%, prunes-40.1%, coriander-11.5%, and fennel-11%.

Larval Performance Study. With the exception of lab diet, all the diets were ground (wheat, barley, soybean, chickpea, pecans, walnut, coriander, and fennel) or cut into small pieces (apricots and prunes) for easy consumption of the food by the larvae. The ground foods were passed through # 40 sieves (Seedburo Company, Chicago, IL) except walnut and pecans that could not be sifted due to their sticky nature caused by the high oil content. About 1g of each of the different foods was weighed separately on a microbalance (Aldinger Company, Dallas, TX) and transferred into a 4.5 cm shell glass vial. Test diets were equilibrated for moisture content for 5-7 d by being held in a chamber containing a saturated solution of sodium chloride (Fisher Scientific, Fair Lawn, NJ) with a relative humidity of ~75%. Single first instar larvae from the laboratory colony and first generation larvae from the mixed wild population were carefully introduced into the glass vials containing the test foods using a camel hair brush. A total

of four blocks over time were conducted in a randomized complete block design. Each block contained 220 vials, ten vials for each of the eleven diets per moth population. A 2.5 cm^2 nylon cloth was placed at the open end of each vial for ventilation and vial caps were tightened on the cloth to prevent the larva from escaping. Air circulation into the vials was allowed by making small holes in the vial caps using a dissecting needle. After the larvae were introduced into the vials and caps securely fastened, they were incubated in a controlled environmental chamber at 28°C, 65-70% RH and 16:8 h (L:D) period. Development of the larvae was monitored at regular intervals and when wandering stage larvae was observed a small strip of cardboard was placed in the vials to provide pupation sites for larvae. Date of adult emergence was recorded. After emergence, the adults were immediately kept in a freezer at -20ºC. The percentage first instar larvae surviving per block was calculated as (number of larvae surviving to adult stage/total number of larvae introduced) x 100, and overall percentage survivability was analyzed over the four blocks. Development time was the time interval between introduction of first instar larva into the vial and emergence of the adult. Adult fresh weights were taken by thawing the frozen adults for about an hour and weighing the samples on a Sartorius microbalance (Aldinger Company, Dallas, TX) to the nearest 0.01 mg.

Oviposition Preferences for Different Diets

No Choice Studies. Oviposition bioassays for field and lab moths were conducted in 5.7 L plastic boxes (Sterilite Inc., Townsend, MA). The lid of the plastic box served as the floor of the arena that was covered with a brown craft paper on which the bottom of a 5-cm diameter glass Petri dish (Fisher Scientific, Pittsburgh, PA) was placed. Foods for the no-choice bioassays were selected based on the developmental

parameters in the performance experiment and were grouped into a) foods highly suitable for larval survival and development (soybean and apricots), b) foods moderately suitable (barley and wheat), and 3) foods unsuitable for larval survival (coriander and walnut). Similar particle size of the foods was ensured by passing the diets through #10 sieve and collecting them on a #14 sieve. Moisture content of the diets was equilibrated by placing the food dishes in a humidifying chamber for 3-4 d at ~75% RH using saturated sodium chloride solution. Five grams of each kind of food was weighed using a microbalance (Aldinger Company, Dallas, TX) and transferred into a 5-cm diameter Petri dish that was placed on the floor of a plastic box. Field moths used for this study were 2nd generation moths from the mixed population of wild adults and raised on the same standard lab diet and under the same environmental conditions as the laboratory moths. Bioassays were conducted in a growth chamber maintained at 28ºC, 60% RH, and 16:8 light-dark conditions. An unmated male and an unmated female (1-2 d old) were released into the plastic box from a small opening on top of the box that was covered with a small piece of duct tape. Eggs laid by the moths were counted after 48 h in the dish, on the box floor, and walls of the arena. Ten replicates were conducted for each moth population in a completely randomized design.

Four Choice Studies. Four-choice preference experiments were conducted in 27.1 L plastic boxes (Sterilite Inc., Townsend, MA). Similar to the no choice studies, the lid of the plastic arena served as a floor and was covered with a brown craft paper. Four 5-cm diameter glass Petri dishes were arranged at about 5 cm from each of the four sides of the box. Three diets, which differed markedly in their ability to sustain laboratory and wild larvae, were selected for this study. Soybean was considered a 'good' diet for larval

survival and development, barley was considered a 'moderately' suitable diet, and coriander was regarded as a 'poor' diet; an empty dish served as control. Diets of similar particle size were prepared and their moisture contents equilibrated as described in no-choice studies. Second generation field moths were used for these experiments. One to 2 d old, virgin male and virgin female moths of a single population were released per box and eggs were counted in the dishes, on the wall, and on the floor of each box after a 48 h period. A total of 10 replications in a completely randomized design were conducted per population.

Statistical Analysis. Percent larval survival data were arcsine square-root transformed to homogenize variances and a 2-factor (population, diet) analysis of variance was performed using PROC MIXED (SAS Institute 2003). Development time and adult fresh weight data were analyzed as 2-factor (population, diet) and 3-factor (population, diet, sex) ANOVA, respectively, after the data were transformed by $\sqrt{(X+0.5)}$ (Zar 1998). Random effects in the above models were the blocks. For oviposition bioassays, egg count data were transformed by $\sqrt{(X+0.5)}$ to normalize variances and the transformed data were analyzed as a single factor (diet) ANOVA for each population separately. Original means are presented in the tables and figures.

Results

Larval Survivability. Laboratory larvae and field larvae differed in their survival on the experimental diets, therefore population by diet interaction was significant ($F = 2.45$; $df = 10, 63$; $P = 0.0153$). No significant differences in the larval survival were observed between the two populations averaged over the eleven diets ($F = 0.63$; $df = 1, 63$; $P = 0.4287$), however, the main effect of diet was very significant ($F = 110.16$; $df = 10, 63$; $P < 0.0001$). Highest survivability of lab larvae was observed on chick pea, wheat, and apricots (Table 1). No significant differences in average survivabilties of laboratory larvae were observed among apricots, soybean, and barley. In the case of field moths, highest larval survivabilities were observed on soybean and apricots, and there were no significant survival differences between wheat, lab diet, and chick pea. Of the foods supporting larval development, prunes were least suitable for survival of both the laboratory and field populations. *P. interpunctella* larvae of the two populations did not survive to the adult stage on walnut, pecan, coriander, and fennel. Comparisons between the populations among the different diets showed that significant differences in larval survivabilties occurred only on chick pea, soybean, and lab diet.

Development Time. The population by diet interaction was not significant ($F = 1.02$; $df = 6, 461$; $P = 0.4131$), implying that the laboratory larvae and the field larvae did not differ in their development times among the different diets. There were no significant differences observed between the two populations ($F = 2.96$; $df = 1, 461$; $P = 0.0861$), but the main effect of diet was significant ($F = 294.85$; $df = 6, 461$; $P < 0.0001$). Laboratory larvae developed fastest on the lab rearing diet and there were no significant differences observed on apricots, soybean, chick pea, and wheat. Development times of larvae

originating from the field population were shortest on apricots, lab diet, and soybean. Slowest development times were observed on prunes and barley for the two populations (Table 2).

Adult Weight. No significant three way (population, diet, sex) interaction was observed (F = 0.85; df = 6, 452; *P* = 0.5335). The mean fresh weights of adults of the two populations were dependent on diet (F = 3.72; df = 6, 452; *P* = 0.0013) and sex (F =7.43; df = 1, 452; *P* = 0.0066). The main effects of population (F = 213.06; df = 1, 452; *P* < 0.0001), diet (F = 33.18; df = 6, 452; *P* < 0.0001), and sex (F = 223.15; df = 1, 452; *P* < 0.0001) were very significant. Laboratory moths weighed more than the field moths and the female weights were significantly higher than the male weights irrespective of the population. Mean adult weights of laboratory males were significantly highest on lab diet (6.47 mg) and soybean (6.09 mg), and lowest on wheat (3.48 mg). There were no significant differences in the mean adult weights of laboratory females on chick pea (10.36 mg), lab diet (9.98 mg), and soybean (9.25 mg), and these mean values were significantly different from the other diets (Table 3).

Field males weighed significantly higher on soybean, apricots, lab diet, and chick pea. Field females raised on soybean weighed significantly higher than females raised on the other experimental diets (Table 3). There were no significant differences in the weights of adult females on chick pea, barley, lab diet, and apricots. Prunes were poor hosts for both laboratory and field larvae since the adults produced on prunes had the lowest weight.

The differences in the mean adult weights between sexes were significantly affected by the diet the larvae fed upon (F = 4.48; df = 6, 452; *P* = 0.0002). Adult males

of the two populations weighed significantly lower than the females on all diets except prunes, where no significant differences were observed. Mean adult weights of field males were significantly different from those of laboratory males on the tested diets with the exception of wheat. Also, there were significant differences in adult weights of females of the two populations on the different diets (Table 3).

No Choice Oviposition Bioassays. In the case of laboratory moths, there were significant differences in the numbers of eggs laid in the dishes with food compared to the dish with no food ($F = 4.70$; df = 6, 63; $P = 0.0005$). Significantly greater numbers of eggs were laid on soybean compared to barley, coriander, and walnut (Fig. 1). There were no significant differences in the average numbers of eggs laid on sorghum, apricots, and wheat. Significantly lower numbers of eggs were laid in empty dishes with no food. The mean total numbers of eggs laid in boxes with the different diets and the empty dish were not significantly different ($F = 1.93$; df = 6, 63; $P = 0.0903$). Furthermore, the females laid a larger percentage of total eggs into a dish with any of the six diets compared to the empty dish, in which case the majority of eggs were laid on the box floor (Fig. 1).

There were significant differences in the mean numbers of eggs laid by the field moths in the food dishes and the empty dish ($F = 7.44$; df = 6, 63; $P < 0.0001$). Soybeans elicited significantly greater oviposition (62.5 eggs) compared to the other diets except barley. Very low numbers of eggs were laid in the empty dish. Mean total numbers of eggs laid in the boxes with the different diets and the empty dish were significantly different ($F = 4.24$; df = 6, 63; $P = 0.0012$). Significantly greater numbers of total eggs were laid in boxes with soybean compared to all other diets and the empty dish except

barley (Fig. 2). Again, when field females laid eggs in boxes with empty dishes, a greater percentage of those eggs were directed outside the dish.

Four-Choice Oviposition Bioassays. Laboratory moths laid significantly different numbers of eggs in the three food dishes compared to the empty control dish ($F = 3.89$; df = 3, 36; $P = 0.0166$). Average numbers of eggs laid in dishes containing soybean and barley were significantly greater from those laid in the empty dish; no statistical significance was observed between eggs counts in dish with coriander and empty dish (Fig. 3). In the case of field moths, average numbers of eggs laid in the food dishes and the empty control were significantly different ($F = 12.08$; df = 3, 36; $P < 0.0001$). The field moths laid significantly greater number of eggs in a dish with soybean compared to barley, coriander, or empty dish (Fig. 4). The mean total numbers of eggs laid per box by field females (43.3±11.1) were lower than the laboratory females (79.2±14.2), but the numbers were not statistically significant ($F = 3.49$; df = 1, 18; $P = 0.0780$).

Discussion

Our developmental bioassays were conducted by introducing individual neonate larvae into small shell vials that precluded the potential effects of conspecific or interspecific competition and intervention by natural enemies. Moreover, the oviposition bioassays were conducted in small plastic boxes under controlled environmental conditions that restricted the movement of the adult moths and offered protection from external interferences by other competing organisms. These artificially narrow environmental conditions were applied to focus just on the scientific questions of host suitability and oviposition preference and to make comparisons between populations

under the same conditions. Therefore, we conclude that 1) laboratory and field populations of *P. interpunctella* differ in their ability to survive, develop, and effectively transform the fed diet into their adult biomass, 2) *P. interpunctella* adults may prefer to oviposit in diets unsuitable for their offspring survival in the absence of favorable larval hosts in no-choice situations, 3) adults from wild populations are more "choosy" when a number of potential hosts are available, ovipositing on foods that are highly suitable for their progeny survival, and 4) laboratory moths are less selective when presented with several hosts of varying quality simultaneously, and oviposit in diets unsuitable for their progeny survival.

Larvae of the two populations survived well on all diets except walnut, pecan, coriander, and fennel. Lab diet was predictably very suitable for the survival of laboratory larvae evident from the high survivability, faster development, and higher adult weight than field moths. As indicated earlier, our laboratory colony of *P. interpunctella* has been cultured on a cornmeal-based diet for several years, and therefore possibly undergone genetic changes and adaptation to the laboratory environment that may be responsible for the observed performance of laboratory larvae on the rearing medium when compared to the field larvae. A majority (> 80%) of the larvae of the two populations survived to the adult stage on apricots, chick pea, soybean, and wheat.

Ground walnut and pecan did not support larval growth, which was surprising because traditionally *P. interpunctella* is a major pest in stored walnuts and pecans (Gecan et al. 1971, Wang and Tang 2001). Furthermore, studies conducted by Nansen and Phillips (2003) found that walnut oil was a strong oviposition stimulant for *P. interpunctella*, and Morrison et al. (2005) showed that whole pecan nutmeat was highly

suitable for the development of *P. interpunctella* larvae. We believe that the main causative factor responsible for the mortality of larvae on walnut and pecan is due to oxidative rancidity caused by the grinding process that probably released high levels of oil. Walnuts and pecans are high in unsaturated fatty acids, and therefore can turn rancid by oxidation to free acids from exposure to air (Musco and Cruess 1954, Maness et al. 1995, Wang et al. 2002). Rancidity of nuts leads to the production of peroxides (Buransompob et al. 2003) and other undesirable compounds that can destroy the nutritive value of the 'exposed' nuts (St. Angelo et al. 1979) and therefore can be detrimental for the survival of the feeding larvae. Our results agree with observations made by Johnson et al. (1992) who showed that ground walnuts were poor hosts for the survival and development of *P. interpunctella* larvae and indicated that the probable reason for this poor performance could be due to rancidity of walnuts caused by grinding. Thus, unknowingly we may have affected the survivability of larvae on walnut and pecan by grinding. Coriander and fennel were unfavorable hosts for the larvae of the two populations. Many spices are known to possess compounds that are insecticidal or prevent feeding by larvae (anti-feedants) (Shaaya et al. 1997). Several species of stored product insects have been shown to be adversely affected by non-polar extracts of spices (Ho et al. 1996, Huang and Ho 1998, Kim and Ahn 2001). Therefore, it was not surprising that the larvae of the two populations did not survive on these two spices.

Development times of the larvae of the two populations were dependent on the diet type. The development times ranged from 28 – 31.5 d on lab diet, apricots, soybean, chick pea, and wheat. Overall, laboratory and field populations did not differ in their development times. Experiments conducted by several researchers have indicated that

the kind of larval diet is probably the most important factor determining the development times of *P. interpunctella*. Allotey and Goswami (1990) showed that the mean development period of a Nigerian population of *P. interpunctella* was highest on wheat (46.11 d) compared to maize, *Zea mays* L., groundnut, *Arachis hypogea* L., and sorghum, *Sorghum bicolor* L. *P. interpunctella* larvae have the shortest development times on cracked or milled soybeans and corn compared to similar sized wheat, rice, *Oryza sativa* L., and black-eyed peas, *Vigna unguiculata* L. (LeCato 1976). Johnson et al. (1992) showed that the development times were the longest on ground walnuts compared to three other test diets. In our development assays, we found that the development times on barley and prunes were the longest. Our results on prunes agree with Johnson et al. (1995), who showed that prunes were poor hosts for *P. interpunctella*. They found that the percentage survival of larvae and the number of adults emerging were the lowest and the development time longest on prunes. Moisture contents of the diets may have played a secondary role in the larval survival and development compared to the chemical composition or nutrient make up of the diets because we observed some contradictory results regarding the correlation of moisture content and development time. For example, moisture content in prunes (40%) was the highest among the diets we tested, but *P. interpunctella* larvae took a long time to complete their development to adulthood. Contrary to this observation, dried apricots had about 33% moisture content and the larvae developed at a faster rate and reached the adult stage in 26 – 30 d. Moisture contents of the other diets on which larvae survived was in the range of 9-11% and the development times were more or less similar except barley, on which larvae developed into adults in about 48 d.

Field adults weighed less than the laboratory adults, and females of the two populations weighed higher than the males. The probable reason for the field adults being lighter than the laboratory adults could be due to the differences in the larval rearing diets. We collected the field moths from pet food and grocery stores and the diets that the field moths developed on were probably lower in quality than the lab-rearing diet, and these field habitats may not have selected for large moths to develop on high quality food. Because the artificial rearing diets are optimized to promote faster development and greater yields of moths, and also due to adaptation of the laboratory colony to controlled environmental conditions, the laboratory larvae have a greater ability to consume food and thus gain weight. Similar to our observations, Carpenter and Wiseman (1999) found that the pupal weights of a wild strain of the corn earworm, *Helicoverpa armigera* (Boddie) (Lepidoptera: Noctuidae), were significantly lower than those of a laboratory strain reared on bean and 'celufil' controls and a corn variety 'SEG25'.

Diet type elicited significant differences in the mean adult weights of field and lab populations, due probably to nutritional factors. Soybean and chick pea were very suitable for the development of the larvae as is evident from the adult weights. Earlier studies by LeCato (1976) showed that mean adult weights of *P. interpunctella* were highest on cracked or broken soybean compared to similar sized corn, wheat, rice or peas. Adult moths from the laboratory colony were heavier when reared on lab diet than the field population. Again, this could be because of the adaptation of the laboratory population to the cornmeal-based rearing diet. Mean adult weights for both the laboratory and field populations were the highest on soybean and chick pea, whose

moisture contents (9-10%) were far lower than those of prunes (40%). Contrary to these observations, we found that adult moths weighed higher on apricots (33 % moisture content) when compared to wheat and barley (10.4-10.9%). Moisture contents of the diets may play a secondary role in the development of larvae and eventual weight gain by the adults compared to the actual nutrient composition (LeCato 1976), such as high fat and protein levels in legumes, and physical form of the foods (Mbata 1990).

In no-choice oviposition bioassays, both the laboratory and field moths oviposited in diets that were unsuitable for their larval survival. The experimental arenas we utilized restricted the dispersal of the females and therefore the moths were probably forced to lay eggs on unfavorable hosts. Adults of the two populations laid greater numbers of eggs on soybean, which was the best larval diet among the diets tested, confirming the notion that the chemical and nutritional composition of the foods is the most important factor determining the post-alightment oviposition behavior of many lepidopterous insects (Ramaswamy et al. 1987, Renwick and Chew 1994). In the oviposition bioassays, we offered the insects diets that were of approximately similar particle size, and clearly moisture content of the diets seems to be of minor importance.

In four choice oviposition assays, laboratory moths were less selective when offered diets of differing quality and larval suitability. They laid eggs in coriander, which was unsuitable for larval survival. There was high individual variation in the oviposition preferences of laboratory adults for the three diets. Total number of eggs laid by the laboratory moths was greater than the field moths. Similarly, olive fruit flies, *Dacus oleae* (Gmelin), reared in the laboratory on an artificial diet for 50 generations laid 3-4 times more eggs compared to conspecific adults reared on olives for 6-8 generations

(Economopoulos et al. 1976). Contrary to the lab-reared *P. interpunctella*, field moths preferred to oviposit in soybean, which was a very suitable diet for the survival of their progeny compared to barley and coriander.

P. interpunctella populations in their natural field habitats can be presumed to be under constant selection pressure from a wide variety of abiotic and biotic factors. Therefore, to increase their fitness by producing successful offspring, wild moths have to oviposit on the best available larval diet. It is clear from our study that ovipositional preferences of field moths for different diets correspond to the suitability of those diets for the survival and development of their progeny. Continuous culturing of *P. interpunctella* in the laboratory may cause physiological and behavioral changes leading to a decline or dilution in their ability to discriminate hosts of varying quality. Raulston (1975) showed that the oviposition patterns of laboratory and wild populations differ in that the laboratory moths oviposited earlier than the wild moths. However, after three generations of artificial rearing of wild moths on an artificial media, the oviposition patterns were similar between those two populations. Evidently, even a few generations of laboratory culturing can cause field-collected moths to lose their typical behaviors exhibited in their natural habitats. We suggest addition of field moths to an existing laboratory colony of moths every 3-4 generations so that sufficient genetic variation and behavioral veracity is maintained. Also, regular tests comparing the lab-reared and wild moths are warranted in order to ensure their behavioral similarity.

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Table 1. Mean percent larval survivabilities (± SE) of two populations of *P. interpunctella* on eleven diets

Diet	Laboratory †	Field †	P^a
Lab diet (control)	100.0 ± 0.0a	85.0 ± 8.7abc	0.0111
Barley	77.5 ± 8.5bc	70.0 ± 14.7cd	0.6033
Wheat	97.5 ± 2.5a	92.5 ± 4.8ab	0.3647
Chick Pea	100.0 ± 0.0a	85.0 ± 5.0bcd	0.0080
Soybean	80.0 ± 7.1bc	97.5 ± 2.5a	0.0052
Apricots	90.0 ± 7.1ab	97.5 ± 2.5a	0.2580
Prunes	67.5 ± 4.8c	67.5 ± 13.1d	0.9117
Pecan	0.0 ± 0.0d	0.0 ± 0.0e	1.0000
Walnut	0.0 ± 0.0d	0.0 ± 0.0e	1.0000
Coriander	0.0 ± 0.0d	0.0 ± 0.0e	1.0000
Fennel	0.0 ± 0.0d	0.0 ± 0.0e	1.0000

†Means followed by the same lowercase letter within a column are not significantly different (N = 4; $P < 0.05$).
[a]Pairwise probabilities comparing survival of the two populations are based on mixed model ANOVA.

Table 2. Mean development times (days ± SE) of two populations of *P. interpunctella* on seven diets[†]

Diet	Laboratory[a]	Field[a]
Lab diet (control)	28.1 ± 0.8d (40)	28.0 ± 2.3de (34)
Barley	48.9 ± 0.9b (31)	46.6 ± 1.6b (27)
Wheat	31.5 ± 0.5c (39)	30.3 ± 0.5cd (36)
Chick Pea	31.4 ± 0.3c (39)	31.2 ± 0.8c (33)
Soybean	29.8 ± 0.6cd (32)	28.2 ± 0.3cde (39)
Apricots	29.7 ± 1.8cd (36)	25.8 ± 0.9e (39)
Prunes	79.7 ± 3.6a (27)	83.7 ± 4.4a (26)

[a]Mean values are based on the number of observations in parenthesis
[†]Means in a column followed by the same lowercase letter are not significantly different ($P < 0.05$)

Table 3. Mean adult weights (mg ± SE) of two populations of *P. interpunctella* reared on seven diets

Diet	Laboratory		Field		Population differences[a]	
	Male	Female	Male	Female	*P* (male)	*P* (female)
Lab diet	6.47 ± 0.48a (17)	9.98 ± 1.07a (23)	3.77 ± 0.20ab (15)	4.89 ± 0.42bc (19)	< 0.0001	< 0.0001
Barley	4.03 ± 0.24bc (21)	7.27 ± 0.62c (10)	2.82 ± 0.29bc (17)	5.12 ± 0.47bc (11)	0.0018	0.0227
Wheat	3.48 ± 0.17c (20)	5.76 ± 0.49c (19)	2.62 ± 0.11bc (15)	4.26 ± 0.31c (22)	0.1535	0.0005
Chick Pea	4.77 ± 0.22b (17)	10.36 ± 0.77a (23)	3.75 ± 0.30ab (21)	5.83 ± 0.61b (13)	0.0036	< 0.0001
Soybean	6.09 ± 0.40a (20)	9.25 ± 1.11a (12)	4.12 ± 0.24a (17)	7.72 ± 0.61a (22)	0.0007	0.0005
Apricots	4.63 ± 0.26b (15)	8.01 ± 0.56b (21)	3.80 ± 0.30a (19)	4.88 ± 0.33bc (20)	0.0196	< 0.0001
Prunes	4.60 ± 0.47b (12)	5.62 ± 0.49c[†] (15)	2.42 ± 0.27c (15)	3.06 ± 0.39d[†] (12)	< 0.0001	< 0.0001
Mean[‡]	4.85 ± 0.15 (122)	8.24 ± 0.34 (123)	3.37 ± 0.11 (119)	5.24 ± 0.21 (119)	< 0.0001	< 0.0001

[†]No significant difference between male and female weights within a population ($P > 0.05$)
[‡]Overall mean adult fresh weights by sex
[a]Pairwise probabilities comparing populations for sex differences are from a mixed model ANOVA
Means followed by the same lowercase letter within a column are not significantly different ($P < 0.05$)

Figure Legends

Fig. 1. Ovipositional responses of *P. interpunctella* females from a laboratory colony in no-choice bioassays. Bars followed by the same lowercase letter or uppercase letter are not significantly different (N = 10; $P < 0.05$).

Fig. 2. Mean (±SE) number of eggs per dish and per box in no-choice bioassays involving field moths. Bars followed by the same lowercase letter or uppercase letter are not significantly different (N = 10; $P < 0.05$)

Fig. 3. Oviposition responses of female *P. interpunctella* from a laboratory colony in response to diets of differing quality in four-choice bioassays. Bars followed by the same lowercase letter are not significantly different (N = 10; $P < 0.05$)

Fig. 4. Mean (±SE) number of eggs laid by females from a field colony of *P. interpunctella* on each diet in four-choice bioassays. Bars followed by the same lowercase letter are not significantly different (N = 10; $P < 0.05$)

Fig. 1.

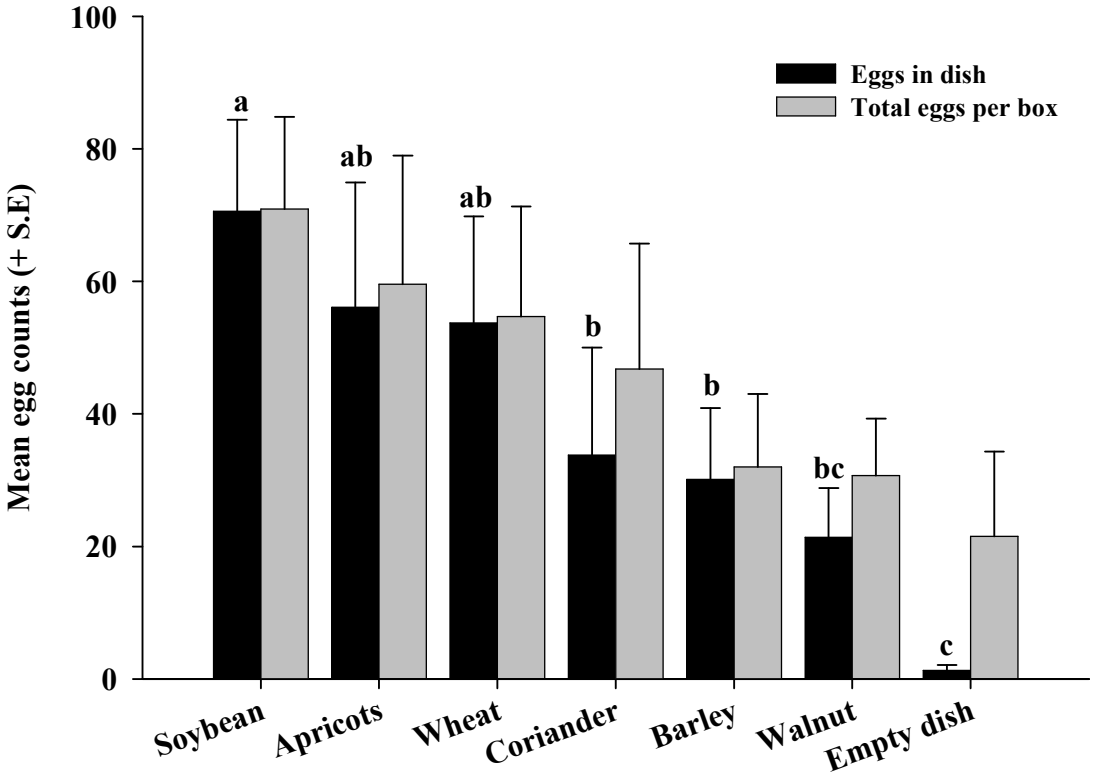

Mean egg counts (+ S.E)
100
80
60
40
20
0
Eggs in dish
Total eggs per box
a
ab
ab
b
b
bc
c
Soybean
Apricots
Wheat
Coriander
Barley
Walnut
Empty dish

Fig. 2.

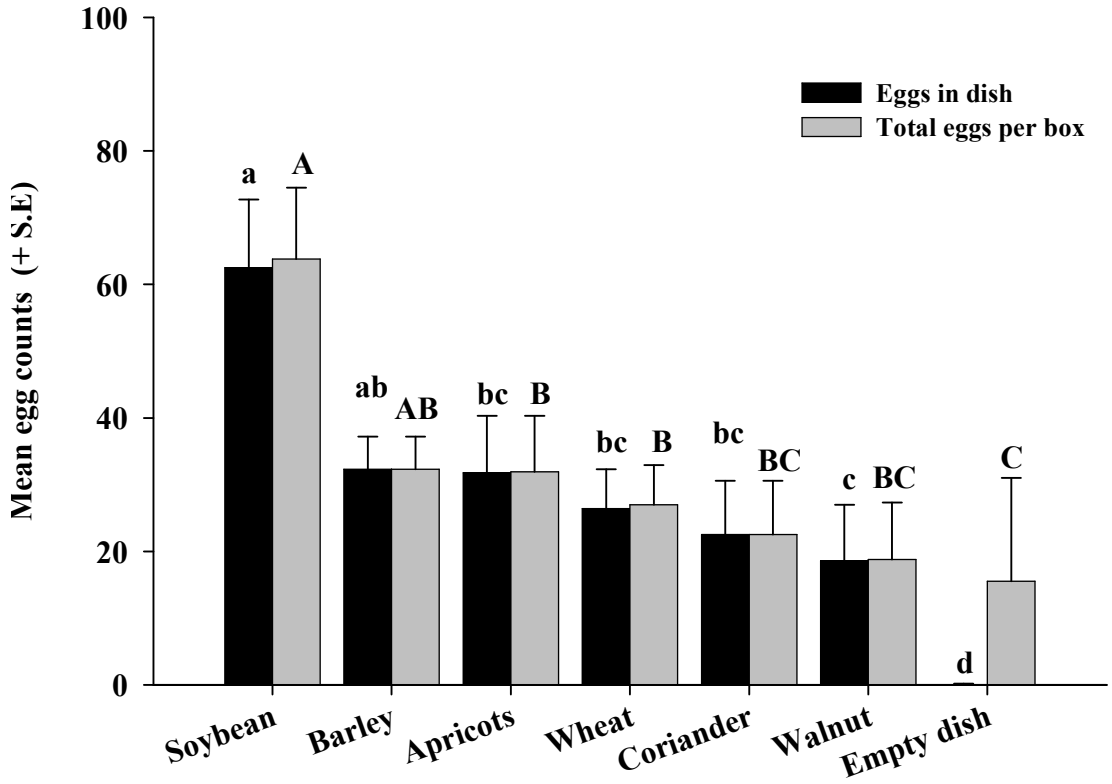

Eggs in dish
Total eggs per box
Mean egg counts (+ S.E)
100
80
60
40
20
0
a
A
ab
AB
bc
B
bc
B
bc
BC
c
BC
d
C
Soybean
Barley
Apricots
Wheat
Coriander
Walnut
Empty dish

Fig. 3.

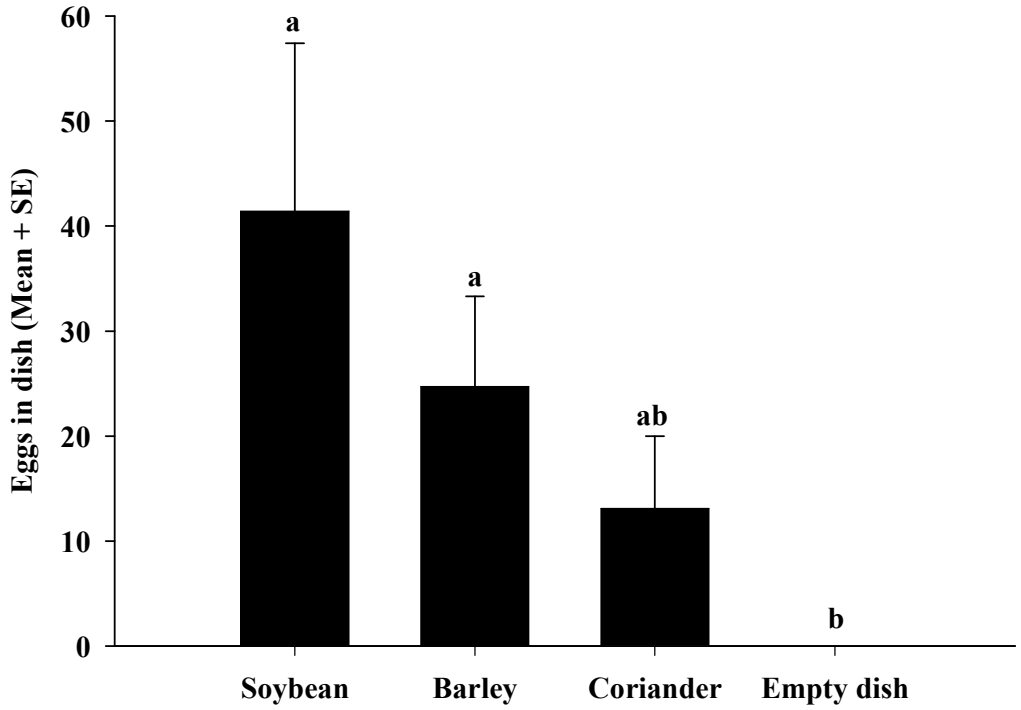
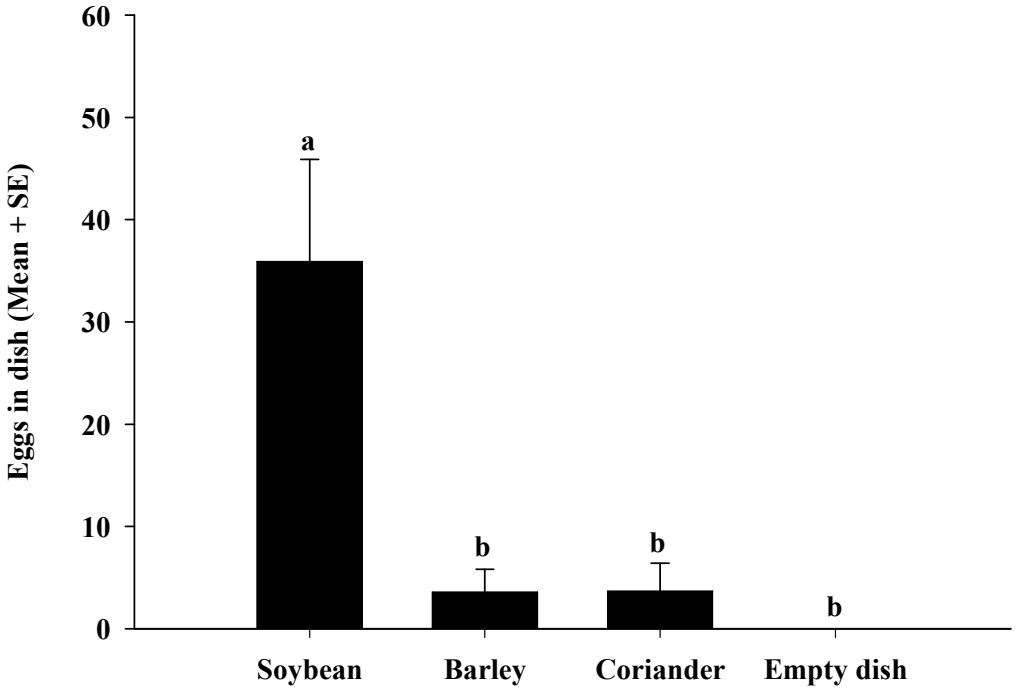

Eggs in dish (Mean + SE)
60
50
40
30
20
10
0
a
a
ab
b
Soybean
Barley
Coriander
Empty dish

Fig. 4.


Eggs in dish (Mean + SE)
60
50
40
30
20
10
0
a
b
b
b
Soybean
Barley
Coriander
Empty dish

CHAPTER IV

RESPONSES OF ADULT *PLODIA INTERPUNCTELLA* (HÜBNER) (LEPIDOPTERA: PYRALIDAE) TO LIGHT AND COMBINATIONS OF ATTRACTANTS AND LIGHT

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Responses of Adult *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) to Light and Combinations of Attractants and Light

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ABSTRACT

The Indianmeal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) is a key pest of stored food products. We studied the responses of *P. interpunctella* adults to 1) ultraviolet (UV), green, and white lights using light emitting diodes, 2) combinations of attractants and green or UV light, and 3) light duration and different scotophase light intensities. Experiments 1 and 3 were conducted in small metal sheds (3.0 x 2.3 x 1.7 m) and experiment 2 was conducted in a larger experimental room (21.4 x 16.5 x 3.0 m). *P. interpunctella* adults preferentially rested on UV-, green-, and white-lighted areas of the metal sheds compared to the corresponding dark areas. UV was the most active of the three lights for positive photo-orientation of the adult moths. A combination of synthetic sex pheromone and green light significantly decreased adult trap captures compared to pheromone alone. Illuminating pheromone-baited traps with UV light did not increase trap captures compared to pheromone-only traps. However, when UV light was placed at the pheromone baited-trap, a slight increase in trap captures was observed. A combination of a food-based attractant and UV light did not increase the overall trap captures compared to attractant only traps. Light traps by themselves were not as effective as pheromone/attractant-baited traps in attracting adult moths. Oviposition studies showed that moths required a period of darkness for maximum oviposition, which was very low when no dark period occurred. Illumination above 8 lux during the scotophase of a 24-hr cycle light-dark caused significant inhibition of oviposition by gravid females.

KEY WORDS oviposition behavior; orientation behavior; sex pheromone; host attractants; photoperiod

Early detection of pest insects causing damage to stored food products is an important component of an integrated pest management strategy in the food industry. Preventive control measures based on reliable early detection tools could have an enormous impact on populations of economically important pests. This is especially true in grain storage areas and food processing plants, where detection of an insect infestation in food for human consumption can accrue huge losses for the producer (Phillips 2006).

The Indianmeal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) is an important pest of stored grain and value-added food products with a worldwide distribution. Larvae feed on a variety of foods such as cereals, beans, nuts, dried fruits (USDA 1975; LeCato 1976; Cox and Bell 1981), dried flowers (Sauer and Shelton 2002), dried vegetables (Na and Ryoo 2000), and some spices (Perez-Mendoza and Aguilera-Penã 2004), and spin silken webs causing economic losses by affecting food quality. Furthermore, the presence of live larvae, larval frass, live adults and their body parts are considered major contaminants in the U. S. food industry (Mason 2003). Qualitative and quantitative losses to food products could be prevented if efficient early detection and pest suppression tools are investigated.

Attraction of insects to light is well known and this behavior has been incorporated as an early detection and monitoring tool for pest insects in the form of light traps (Gilbert 1984). Three characteristics of light that can affect the behavior of an insect are 1) light quality or wavelength, 2) light intensity, and 3) light duration (Callahan 1957). As is the case with most insect pests infesting stored foods, *P. interpunctella* adults have been shown to differentially respond to various wavelengths of electromagnetic radiation. Studies conducted by Stermer (1959), using 9 µW light bulbs,

showed that *P. interpunctella* adults were attracted to light wavelengths in the range of 334 -546 nm and that the most attractive radiation range was 334-365 nm. Soderstrom (1970a) tested different numbers and shapes of green electroluminescent light bulbs and single circular ultraviolet lamps with suction traps and found that eight 0.06 W green lights per trap versus a single circular 32 W ultraviolet (UV) lamp significantly increased the trap catches of *P. interpunctella*. These observations contradict findings by Stermer (1959) probably because of differences in design and light intensities of light devices. Kirkpatrick et al. (1970) found that a suction trap containing a combination of 0.3 W green light and circline 32 W black light did not increase the trap catches of *P. interpunctella* compared to green or UV light alone. Apart from the above three studies, no experiments have been conducted to test the responses of *P. interpunctella* to light quality. Earlier light trapping studies involved attraction of mixed populations of *P. interpunctella* adults toward light sources, ignoring the potential importance of reflected light in attracting or repelling adult moths (Kirkpatrick et al. 1970, Soderstrom 1970a). Understanding the orientation behavior of adult moths toward reflected light and direct light from novel light sources such as light emitting diodes (LEDs) could be quite useful in developing inexpensive, non-chemical methods of insect pest control. Although traps baited with the synthetic female sex pheromone, *(Z, E)* 9, 12 tetradecadien-1-yl acetate (ZETA) of *P. interpunctella*, are reliable indicators of severity of pest infestations, a combination of pheromone traps with attractive light sources could provide a more effective trapping strategy for monitoring pest populations.

Duration of light, or photoperiod, plays an important role in the flight and oviposition behavior of *P. interpunctella* (Lum and Flaherty 1970; Mbata 1985). The

onset of darkness serves as a stimulus for the nocturnal movement of the females and peak oviposition occurs immediately after a phase shift from light to dark (Madrid and Sinha 1982). However, there is no information on the effect of different scotophase light intensities on oviposition by *P. interpunctella*. According to Driesig (1980), responses of nocturnal insects to scotophase illumination is an "all-or-none" response, suggesting that a threshold light intensity is required during the dark phase, which when exceeded would inhibit typical behaviors characteristic of nocturnal insects. Therefore, we investigated the effect of different scotophase light intensities on ovipositional response of *P. interpunctella*.

The objectives of this study were to 1) evaluate the spatial distribution and trap captures of virgin males, virgin females, and mated females in response to three colored lights in small metal sheds, 2) study the combinatorial trapping efficacy of ZETA/food-based attractant and light to adult moths, and 3) study the oviposition behavior of *P. interpunctella* under different light conditions and scotophase light intensities.

Materials and Methods

Insects. The insects for all the experiments were obtained from a laboratory colony of *P. interpunctella* reared on a standard diet (Phillips and Strand 1994). Cardboard rolls that served as pupation sites for the wandering 5th instar larvae were placed in the colony jars when they were observed. After a week, the rolls were removed from the colony jars, and pupae were separated by sex, placed singly into 4.5 cm glass vials, and adults emerging from the pupae were used for experiments that required moths of a specific age.

1. Spatial Orientation of Moths to Lights in Small Metal Sheds. Green (525 nm), UV (395 nm), and white (450 nm –700 nm) light emitting diodes (LEDs; 5 mm, 12 V, 30° radiation angle; The LED Light Inc., Carson City, NV) were used for these experiments, which were conducted under otherwise continuous dark conditions. LEDs were used because they provided point sources of narrow beam high intensity radiation, they were easy to use, and were long-lasting. Preliminary experiments showed that moths preferentially rested on low light-illuminated horizontal and vertical surfaces that reflected light from a light source on the floor, compared to dark surfaces. Therefore, experiments were conducted in three closed metal sheds, 3.0 m x 2.3 m x 1.7 m, to evaluate the orientation and spatial distribution of virgin males, virgin females, and mated females separately in response to the lighted regions versus dark regions of experimental sheds. Cracks and crevices inside the sheds were plugged using a foam sealant in order to prevent external light from entering the experimental arena.

Sheds were marked into two equal halves using a white tape along the center line, and a white sheet of cardboard that served as a rectangular trap (36 cm x 15 cm), with adhesive glue over an area of 285 cm^2 on its top surface, was placed in each half of the metal shed and oriented parallel to the center line. The two traps were 1.8 m apart and each trap was ca. 0.6 m from the nearest side wall. Two LEDs were inserted through holes located along the length of each sticky 'light' trap about 10 cm apart, and traps with no LEDs were controls. Each trap was placed on a metal stand that raised it 10 cm above the floor, with the sticky portion of the trap and the LEDs facing the ceiling. Therefore through this arrangement, one-half of the metal shed was lighted (transmitting light from

the LEDs that reflected from the inside shed surface on that side) and one-half of the shed had no light source and was dark.

Thirty moths (< 3 d old) were released at a given time in each metal shed and the spatial distribution of resting moths and numbers of moths captured in sticky traps were recorded after 24 h. When mated females were used, they were obtained by releasing groups of <3 d old virgin males and females into a small screened cage (approximately 30 x 30 x 30 cm) and collecting the adults *in copula* singly into 4.5 cm glass vials. The mated females were separated from males the following day into clean shell vials and were used for the experiments.

Resting moth counts to determine spatial distribution on the 'dark' and 'light' side of the shed were recorded by counting the number of moths on the floor, walls and ceiling, and included the moths caught in the trap in the respective half of the shed. In addition to spatial distribution, trap capture data were analyzed separately to evaluate the orientation of adult moths directly to light sources. The positions of the lighted vs. dark traps were alternated each time the light treatments were randomly assigned to the three sheds to avoid biased results due to location of the treatments. Temperature and relative humidity were recorded using Hobo® data loggers (Onset Computer Corporation, Bourne, MA), and varied from 28°-35ºC and 25-30%, respectively, during the course of the study. Temperature and humidity conditions were similar in all three sheds for a given time period and were affected by ambient conditions in the building where the sheds were placed for this experiment. A total of five replications, blocked over time, were conducted each for separate experiments with virgin males, virgin females, and mated females in a randomized complete block design.

2. Orientation of Moths to Combinations of Semiochemicals and Light. The responses of *P. interpunctella* adults to the sex pheromone ZETA and a food-based attractant in combination with green or UV light were tested in four-choice trapping experiments under dark conditions. The experiments were conducted at three locations in an enclosed basement room, 21.4 x 16.5 x 3.0 m^3, on the campus of Oklahoma State University, Stillwater, OK (Fig. 1). Diamond shaped sticky traps (Storgard® II, Trécé Inc., Adair, OK) were used for the series of experiments. The temperatures and relative humidities throughout the course of the studies ranged from 24-32°C and 23-35 %, respectively.

In case of males, we tested green LEDs (525 nm) initially in combination with ZETA by focusing green light on ZETA-baited traps containing a rubber septa (Sleeve Stopper 03-215-5, Fisher Scientific, Pittsburgh, PA) impregnated with 200 µg of ZETA (Bedoukian Research, Inc., Danbury, CT) in 5 µL hexane. Each block included four treatments, 1) blank trap, 2) light only trap, 3) ZETA only trap, and 4) Light + ZETA trap. The traps were hung 2.0 m from the ground and located on or near a wall or vertical support column. A 3-LED strip (3.0 V; 90° radiation angle; The LED Light Inc., Carson City, NV) was used as the source of light; the light strip was suspended at a distance of 0.6-0.8 m from the trap, at the same height as the trap, and illuminating the trap. The sticky traps were arranged in such a way that the distance between the traps was 3.3-5.5 m. For this and subsequent trapping experiments described below, about 200 moths of mixed age and sex were released from a single colony jar at each trap-block location by keeping the colony jar open for 6 h. Trap captures were counted after 48 h. The

experiment was conducted over three different 48 h periods for a total of nine replications per treatment, and each time the position of the treatments was randomized.

In the second experiment, ultraviolet LEDs (12 V; 30° radiation angle; The LED Light Inc., Carson City, NV) replaced the green lights in the previous experiment. The basic experimental set up was the same as the green-light experiment except that a single UV LED was used per light treatment. The trap counts were taken after 48 h. Because we found that the UV light attracted the females in the metal shed experiment, we checked the traps for the presence of females in this experiment. A total of nine replications over three experimental periods were conducted. A final experiment with ZETA involved a UV LED being placed on top of the trap, such that light was being emitted from the trap, rather being reflected from light illuminating the trap from a distance. The UV LED was not placed inside the trap to avoid possible degradation of ZETA by exposure to UV light (Bruce and Lum 1976, 1981). The design was identical to the previous two experiments. Nine replicates were conducted.

Attractiveness of a food-based attractant (the same as that used in Moth Suppression®, Insects Limited Inc., Westfield, IN; patent-pending) was tested in combination with UV light. Four ml of the food-based attractant solution was applied to a single cotton wick that was placed in a sticky trap alone or in combination with UV light that was placed on top of the trap. The four treatments per block included 1) blank trap, 2) light only trap, 3) attractant-baited-trap only, and 4) light + attractant trap. As with previous trapping experiments with ZETA, trap captures were recorded after 48 h. A total of 8 replications was conducted, and captures of males and females were recorded.

3. Oviposition in Response to Light Duration and Intensity. The oviposition studies were conducted in rectangular glass containers (60 cm x 30 cm x 41 cm) that were housed in the metal sheds described above. Two glass containers were arranged on a plywood sheet (100 cm x 50 cm) separated by 20 cm and raised 10 cm above the floor using two metal stands. About 15 g of wheat kernels (hard red winter wheat, *Triticum aestivum* L.) were added to an opened 5 cm diameter plastic Petri dish (50 mm x 10 mm) that was placed in the center of each glass chamber. Two male-female pairs of virgin moths (<2 d) were released in each experimental arena between 0800-1400 h local time and the numbers of eggs laid were counted after 72 h. Lighting was provided by a single 100 W (Sylvania Soft White, Osram Sylvania Company, Danvers, MA; experiment a) or two 100 W incandescent bulbs (experiment b and c).

a. Effect of Photoperiod on *P. interpunctella* Oviposition. There were three treatments for this experiment, 1) 24 h light, 2) 16 h of light and 8 h of dark, and 3) 24 h dark. A timer was connected to a single 100 W incandescent bulb that was clamped to the ceiling, to provide 16 h of light for treatment 2. The three treatments were assigned randomly to the three sheds, each of which contained two glass containers. Therefore for each experimental time period of 72 h, there were two observations for each treatment. The treatments were randomized between the sheds each time the experiment was repeated. A total of ten replicates were conducted. Temperatures in the metal sheds ranged from 23-27ºC during the course of the experiments.

b. Effect of Low Light Intensity During the Dark Period on *P. interpunctella* Oviposition. It was evident from experiment 1 that the females require a dark period during a daily cycle to realize their full oviposition potential. The objective of this

experiment was to examine the effect of increasing light intensity during the scotophase on oviposition by *P. interpunctella*. Two 100 W incandescent bulbs (Sylvania Soft White, Osram Sylvania Company, Danvers, MA) were clamped on to the ceiling (1.7 m high) of each of the two metal sheds. There were two treatments as follows: i) 16 h photophase and 8 h of 'dim' light scotophase, and ii) 16 h photophase and 8 h of 'dark' scotophase (control). The two light bulbs were used such that one full intensity light bulb operated for 16 h and the other 'dim' light bulb either operated for 24 h (i) or for 16 h (ii). The 'dim' light intensity was obtained by connecting one of the light bulbs to an incandescent light dimmer (Lutron Maestro®, Lutron Electronics, Inc., Coopersburg, PA). It is not known if the reduction in light intensity caused any changes to the spectral characteristics of light from the incandescent light source. In the first trial, light intensity from the incandescent "dim" bulb was adjusted such that the light level was too low to be detected by a light meter, but it was barely visible to the human observer. The two glass containers were arranged in such a way that they were directly under the light source and a light intensity recorder (Hobo® pendant data logger, Part# UA-002-08, Onset Computer Corporation, Bourne, MA) was placed between the two glass containers. These two treatments were randomly assigned to two sheds and the positions of the two treatments were alternated for each repetition of the experiment. A total of 10 replications were conducted for each treatment. In the second trial, the light intensity during the dark phase was increased by adjusting the dimmer control to provide light intensity in the range of 11-22 lux at the level of the light meter that was positioned between the glass containers. The light intensities on the floor and top of the arena were 8 lux and 40 lux, respectively. The basic set up of the experiment was the same as the previous experiment. Eight to 10

replications were conducted and the temperatures in the metal sheds ranged from 28ºC - 33ºC.

Statistical Analysis. The number of moths counted on the lighted side of the shed in orientation experiments was converted into percent of total moths per shed and these percentage values were compared among the three treatments. The percentage data were arcsine square root-transformed (Zar 1998) and analyzed by PROC MIXED (SAS Institute, Cary, NC). Similarly, within an individual metal shed, percent moth distributions in the lighted and dark side of the metal shed were calculated and analyzed by Chi-square test in a contingency table (PROC FREQ). Trap captures in the metal sheds were analyzed between the three treatments by the differences in number of moths caught in the light trap and blank trap (Δ light – blank) by Kruskal-Wallis test. Wilcoxon signed-rank test was used to analyze trap capture differences between the light trap versus the blank trap for each light treatment. Trap capture data from the light+semiochemical combinatorial study were transformed using $\sqrt{(X+0.5)}$ and analyzed as a 2 x 2 factorial ANOVA (light and attractant, each factor with two levels). The number of males and females trapped in combination experiments were compared by PROC TTEST of SAS. Egg count data from oviposition studies were also transformed by $\sqrt{(X+0.5)}$ and the transformed data was analyzed by PROC MIXED (SAS Institute 2003); blocks (dates) were considered random effects in the analysis. All data presented are untransformed means + standard error of the mean.

Results

Spatial Distribution and Trapping Study. A significantly greater percentage of males were found resting in the green-lit regions of the metal sheds compared to UV and

white lighted regions (F = 8.74; df = 2, 12; $P = 0.0045$). There were no significant differences in the numbers of moths found in the UV and white lighted regions of the sheds (Fig. 2). Males were significantly found resting on green ($\chi^2 = 166.12$, df = 1, $P < 0.0001$), UV ($\chi^2 = 24.11$, df = 1, $P < 0.0001$), and white ($\chi^2 = 27.01$, df = 1, $P < 0.0001$) lighted sides of the metal sheds compared to their corresponding dark sides. Among the three different light traps, no significant differences in male captures were observed ($\chi^2 = 3.51$; df = 2; $P = 0.1945$). However, significantly greater number of males were attracted to green ($\chi^2 = 8.33$, df = 1, $P = 0.0039$), UV ($\chi^2 = 6.07$, df = 1, $P = 0.0138$), and white ($\chi^2 = 5.63$, df = 1, $P = 0.0177$) light traps compared to their respective control traps with no light.

In the case of unmated females (Fig. 3), percentage unmated females distributed on the lighted side of the shed was not significantly different among green, UV, and white lighted regions (F = 3.79; df = 2, 8; P = 0.0696). Significantly greater percentage of moths were observed on the green-($\chi^2 = 134.99$; df = 1; $P < 0.0001$), UV-($\chi^2 = 20.0$; df = 1; $P < 0.0001$), and white- ($\chi^2 = 56.18$; df = 1; $P < 0.0001$) lit regions of the respective metal sheds compared to their corresponding dark regions. Among the three light traps, significantly greater numbers of unmated females were attracted to UV light trap than to green and white light traps ($\chi^2 = 9.25$; df = 2; $P = 0.0033$). No significant differences in trap captures were observed for green and white light traps ($\chi^2 = 1.03$; df = 1; $P = 0.3092$). There were no significant differences observed in the number of moths trapped in green light trap versus control ($\chi^2 = 3.72$; df = 1; $P = 0.0539$) and white light trap versus the control trap ($\chi^2 = 2.25$; df = 1; $P = 0.1336$). Significantly greater numbers of

unmated females were trapped in the UV light trap compared to the control trap (χ^2 = 7.31; df = 1; P = 0.0069).

There were no significant differences in the percentage of mated female moths (Fig. 4) observed in the green, UV or white-lit regions of the metal sheds (F = 0.37; df = 2, 12; P = 0.6994). Significantly greater percentage of mated females were observed in the green-(χ^2 = 97.86; df = 1; P < 0.0001), UV-(χ^2 = 103.97; df = 1; P < 0.0001), and white-(χ^2 = 58.07; df = 1; P < 0.0001) lit regions of the metal sheds when compared to their respective dark regions. Mated females were more highly attracted to the UV light traps than to the green and white light traps and these trap captures were significantly different (χ^2 = 10.81; df = 2; P = 0.0002). Fewer mated females were caught in green and white light traps and the trap captures were not significant different (χ^2 = 2.0; df = 1; P = 0.1563). Within the respective metal shed, more mated females were caught in green (χ^2 = 6.0; df = 1; P = 0.0143) and UV (χ^2 = 7.31; df = 1; P = 0.0069) light traps versus the control traps. No significant differences in trap captures between the light and control trap were observed for white light (χ^2 = 0.06; df = 1; P = 0.8111).

Combinatorial Trapping Study. In the green light experiment, no significant interaction effect of light and ZETA was observed (F = 3.67; df = 1, 30; P = 0.0648). The main effect of ZETA was highly significant on trap captures of males (F = 108.0; df = 1, 30; P < 0.0001), however, the main effect of light (F = 3.67; df = 1, 30; P = 0.0648) was not significant. Focusing green light on ZETA-baited traps significantly reduced trap captures compared to ZETA alone traps, and green light only traps were no more attractive than blank traps (Fig. 5).

When UV light illuminated the pheromone trap from a distance, no significant differences in male trap captures were observed between ZETA only trap and light+ZETA trap, but these captures were significantly different from trap captures in light only traps and blank traps (Table 1). The light by ZETA interaction and the main effect of light were not significant ($P > 0.05$); the main effect of ZETA was highly significant (F = 184.41, df = 1, 30, $P < 0.0001$). There were significant differences in female captures between light only versus blank traps, but these light trap catches were not significantly different from ZETA only or light+ZETA traps. Only the main effect of light was significant in case of females (F = 4.60; df = 1, 32; $P = 0.0397$). There were significant differences in the numbers of males and females caught in ZETA only trap and UV+ZETA traps. In the case of total trap captures, the interaction effect of light by ZETA (F = 4.10; df = 1, 30; $P = 0.0519$) and the main effect of light were not significant (F = 0.01; df = 1, 30; $P = 0.9353$); the main effect of ZETA was highly significant (F = 153.5; df = 1, 30; $P < 0.0001$).

When UV light was placed on a ZETA-baited trap, a small but non-significant increase in male trap captures compared to ZETA alone traps was observed. Male trap captures in ZETA only and light+ZETA traps were significantly different from captures in light only or blank traps (Table 2) Only the main effect of ZETA was significant (F = 23.73; df =1, 32; $P < 0.0001$). Significantly greater numbers of females were caught in light trap and light+ZETA trap when compared to blank trap. The main effect of light for female captures was significant (F = 5.07; df =1, 30; $P = 0.0318$). There were significant differences in the number of males versus the females trapped only in ZETA trap and light+ZETA trap (Table 2). There were no significant differences in the total numbers of

moths caught in the ZETA only and light+ZETA traps. Two-way ANOVA for total moths caught showed that the non-significant effects in the design were light by ZETA interaction (F = 0.40; df = 1, 32; $P = 0.5324$) and light (F = 1.17; df = 1, 32; $P = 0.2877$), and the significant main effect was ZETA (F = 21.81; df = 1, 32; $P < 0.0001$).

In the experiment involving the food-based lure, trap captures of males in light only, attractant only, or light+attractant traps were not significant (Table 3). The significant effects in the two-way analysis for males were the light (F = 6.88; df = 1, 28; $P = 0.0139$) and the attractant (F = 8.90; df = 1, 28; $P < 0.0058$). Female trap captures were statistically significant between light only traps and attractant only and attractant+light traps. The only significant effect for female trap captures was the main effect of attractant (F = 28.1; df = 1, 28; $P < 0.0001$). Significantly greater numbers of male moths were trapped in UV light trap than the females (Table 3). Overall trap captures between the attractant only and light+attractant were not significant (Table 3). There were significant differences in total trap captures between attractant only and light only traps. The interaction effect of light by attractant (F = 3.65; df = 1, 28; $P = 0.0664$).and the main effect of light (F = 2.73; df = 1, 28; $P = 0.1094$) were not significantly different, however, the main effect of attractant was highly significant (F = 21.87; df = 1, 28; $P < 0.0001$).

Oviposition Studies. Continuous light (24 h L) significantly reduced oviposition by *P. interpunctella* females (Fig. 6; F = 5.74; df = 2, 27; $P = 0.0084$). No significant differences in the numbers of eggs laid during 16 h L: 8 h D and 24 h dark were observed, although fewer eggs were laid during 24 h dark compared to 16 h L: 8 h D conditions. A scotophase light intensity of ~8-40 lux corresponding to the dark phase

significantly reduced oviposition (Fig. 7; F = 6.37; df = 1, 16; *P* = 0.0226). However, when the light intensity was further reduced to levels undetectable by a light meter but faintly visible to the human observer, no significant differences in oviposition occurred between dim light and totally dark scotophase conditions (F = 0.92; df = 1, 14; *P* = 0.3550) (Fig. 8). This suggests a certain level of scotophase light intensity that the females can tolerate, exceeding which oviposition is inhibited.

Discussion

Studies in the metal sheds showed that a significant percentage of adult moths moved to areas of low illumination compared to the darker regions for all the three colored light treatments. Males settled significantly on the green illuminated areas of the shed compared to the UV and white-lit regions, and they prominently rested on the lighted side of the sheds compared to the dark regions. In case of females, there were no significant differences in the number of moths settling on the lighted side of the sheds among the three treatments, and the lighted side significantly attracted more females compared to the respective darker regions. Likewise, Henneberry and Howland (1966) found that about 43% of males of the cabbage looper moth, *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae), preferentially rested on the UV illuminated area of the experimental arena compared to none in the dark. The behavioral mechanisms and adaptive causation, if any, involved in this kind of preferential resting of *P. interpunctella* on low-lit areas are not known.

Our trapping studies in small sheds showed that *P. interpunctella* adults respond more positively to a UV light source than to green or white lights. Although trap captures of males and females were not compared, females seemed to show a greater

response to UV light than males in a close range situation. Our observations concur with Stermer (1959) who found that *P. interpunctella* adults were more attracted to the UV portion of the light spectrum compared to wavelengths in the visible portion. Trapping studies by Kirkpatrick et al. (1970) and Soderstrom (1970a) showed that *P. interpunctella* adults were more attracted to green lights than to UV light sources. Our results differ from observations by Kirkpatrick et al. (1970) and Soderstrom (1970a) presumably because of their using light devices of different design and intensity, and varying the intensity of light has been shown to attract or repel several species of stored product beetles (Soderstrom 1970b). We used 12 V LEDs that provided point sources of spectrally pure, concentrated light emitted in a 30 - 90° radiation angle and emit significantly less amount of light compared to higher wattage light bulbs.

Insect color vision has been a subject of intensive research and by far the most studied insects in this regard are pollinators such as the honey bee (Von Frisch 1967; Labhart 1974). Many species of insects, including several lepidopterans, have a conserved set of UV, blue, and green photoreceptors in their eyes (Briscoe and Chittka 2001). In the case of *P. interpunctella*, electroretinogram (ERG) studies by Marzke et al. (1973) showed that peak spectral sensitivities were in the blue (450 nm) and green (550 nm) regions of the light spectrum and responses in the UV region (350-400 nm) were more subdued. This earlier work suggests the presence of blue and green photoreceptor cells in *P. interpunctella* eyes, although, the presence of UV receptors cannot be discounted because sensitivities of different areas (dorsal, ventral, and dorsal rim) of an insect eye differ to incident light (Stavenga 1992, White et al. 2003; Stalleicken et al. 2006) and Marzke et al.'s (1973) study did not clearly emphasize the area of eye that was

probed for recording responses. We found in the current study that UV light elicited more orientation by adult Indianmeal moths compared to green light, which is contrary to what would be expected from the results of the ERG studies done by Marzke et al. (1973). However, electro-physiological studies only involve recording the perception and transfer of electrochemical stimuli by the peripheral sensory cells and do not involve the central nervous system or necessarily correlate directly to behavior. A negative or positive phototactic behavioral response is the result of perception of stimuli by the sensory cells and processing of this information by the brain (Antignus 2000). Therefore, responses of sensory cells observed in electroretinogram studies may not effectively transcribe into behavioral responses of insects.

Then why are *P. interpunctella* adults attracted to UV light? Although no conclusive evidence of adaptive evolution exists for photo-orientation by *P. interpunctella*, a possible reason could be that shorter wavelengths of light might induce migratory or dispersal behavior in insects by providing escape routes through empty spaces (Scherer and Kolb 1987a, b). As humans began storing food in enclosed areas shielded from outside environment during relatively recent geological history, *P. interpunctella* has also probably recently evolved to be a pest of stored foods. There is a possibility that because of their dark habitats, adult moths trying to escape from a spent or unfavorable resource may have encountered intermittent open spaces toward the sky. Because the day sky is UV "rich" (Silberglied 1979), and moon light has similar spectral composition as sun light (Stair and Johnston 1953), the adult moths might have adapted to being attracted to UV portion of light. An alternative, or perhaps additional, hypothesis for moth responses to UV light is that such light is reflected from green plant

tissues, and visual response to plants could be adaptive for phytophagous insects (Prokopy and Owens 1983). *P. interpunctella* is clearly phytophagous in the storage habitat, feeding on grains and grain products, and it may have utilized other plant tissues with short-wave length reflectance prior to evolution to the storage habitat. Virtually nothing is known about the distribution of photoreceptors and sensitivities of different regions of an adult eye in *P. interpunctella*. Further research into visual ecology of adult moths would be useful in understanding the behavioral responses of *P. interpunctella* to light, and possibly would help in developing non-hazardous population control strategies.

Our results with combinatorial experiments involving sex pheromone and light that had no measurable increase in response, and mostly had a reduced response to the combination, are similar to findings from other insects. Research conducted by Burkett et al. (1998) showed that traps with CO_2 as attractant and equipped with colored LEDs or incandescent lights did not cause an overall increase in trap catches of several species of mosquitoes. A significant decrease in trap captures, compared to 'no light' controls, was observed for *Aedes dupreei* (Coquilett) (Diptera: Culicidae) when green, yellow, or incandescent light was used along with CO_2 attractant traps. The possible reasons for the variable responses of adult moths to green reflected light in this study and to those in metal sheds could be due to the differences in reflectance characteristics of metal and concrete, presence of mixed ages and sexes among the released moths, and greater intensity of green LEDs used for the combination study. When UV light was focused on ZETA-baited trap, lower but non-significant trap catches compared to ZETA only trap were observed. However, a slight increase in male trap captures was observed when the UV light source was placed on top of pheromone trap. Again, light only traps were not

as effective as the pheromone-baited traps in capturing adult moths. It is apparent from these combinatorial experiments involving ZETA and light that low illumination of traps with green/UV lights or a combination of UV light and pheromone does not significantly increase male trap captures, and this may simply be due to ZETA being a stronger stimulant to male *P. interpunctella* than light when presented together. Conversely, Henneberry and Howland (1966) and Henneberry et al. (1967) found that *T. ni* pheromone-baited traps fitted with black light (UV) traps significantly increased male trap captures compared to either traps alone. Henneberry et al. (1967) also found that increasing the numbers of females per black light trap significantly increased trap catch. Pheromone-baited traps were far more efficient in catching males of the Egyptian cotton leafworm, *Spodoptera littoralis* (Boisd.) (Lepidoptera: Noctuidae) than UV light traps (Rizk et al. 1990). We found that significantly more males were caught in the UV light trap than females when a food-based attractant was used. This is probably because the food attractant was not as powerful as the sex pheromone in attracting males, and there may have been a food+UV combination effect for increased male response. Barr et al. (1963) found that the intensity of colored lights is the most important factor in attracting insects, but we did not investigate variable light intensity on our orientation experiments. Further research needs to be conducted to study the combined effect of UV lighting devices of different intensities, and different semiochemical types and concentrations on trap captures of male and female *P. interpunctella*.

Oviposition experiments with different photoperiods confirmed earlier findings (Lum and Flaherty 1970; Mbata 1985), which showed that continuous light inhibits oviposition by *P. interpunctella*. Females have been shown to display erratic oviposition

behavior when exposed to 24 h light conditions (Madrid and Sinha 1982). *P. interpunctella* females preferred to lay eggs under alternate light-dark periods or 24 h dark conditions. One exception to this behavior has been reported by Bell (1981) who found that some populations of *P. interpunctella* laid eggs during the light periods. Gravid females seem to respond to a significant decrease in light intensity during light-dark transition and require some period of darkness for eliciting oviposition. At a light intensity of 8-40 lux, oviposition was inhibited, however, under very low light conditions (>0 to <8 lux), oviposition was similar to that under dark scotophase conditions. Therefore, *P. interpunctella* females can tolerate a certain threshold light intensity during the scotophase that when exceeded will inhibit oviposition. In a related stored product pyralid moth, *Cadra cautella* (Walker), decreasing light intensity and temperature during dusk have been implicated in inducing oviposition (Steele 1970; Hagstrum and Tomblin 1972). *C. cautella* females require a light intensity of 0.5-2.0 lux for maintaining an oviposition rhythm. Madrid and Sinha (1982) showed that for inducing nocturnal flight behavior in *P. interpunctella* females required an intensity range of 0.2-2.9 lux. In our study, although the absolute light intensity at the level of the insect was not known, the threshold range for oviposition (>0 – 8 lux) was similar to that required for nocturnal flight behavior of *P. interpunctella*.

Our experiments clearly show that adult moths will orient to low illuminated surfaces and they are very attracted to UV light when pheromone or other strong attractants are lacking. Pheromone was more attractive to males than UV light, and UV light may have reduced response to pheromone, so the use of pheromone-baited traps alone is recommended as a monitoring tool for *P. interpunctella* compared to

UV+pheromone traps or UV light traps. Our oviposition studies suggest that food storage environments in which lights are kept 'on' 24 h a day will result in less infestation by *P. interpunctella* than storages in which lights are always off or in which there is a light and dark cycle. Future research should focus on understanding the visual ecology of *P. interpunctella* adults so that sustainable management strategies could be developed.

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Table 1. Trap captures (mean ± SE) of *P. interpunctella* adults in unbaited and baited traps illuminated with UV light from a distance[†]

Treatment	*n*	Male	Female	*P* (sex)[a]	Total
Blank	9	0.0 ± 0.0b	0.0 ± 0.0b	-	0.0 ± 0.0b
UV	9	0.2 ± 0.1b	0.7 ± 0.2a	0.1324	0.9 ± 0.3b
ZETA only	9	14.2 ± 2.8a	0.2 ± 0.1ab	< 0.0001	14.4 ± 2.9a
UV + ZETA	9	10.6 ± 1.9a	0.3 ± 0.2ab	< 0.0001	10.9 ± 1.9a

[†]Means followed by the same lowercase letter within a column are not significantly different ($P < 0.05$)
[a]Pairwise probabilities for differences between sexes were computed by t-test

Table 2. Trap captures (mean ± SE) of *P. interpunctella* adults in unbaited and baited traps with UV light on top of the trap[†]

Treatment	*n*	Male	Female	*P* (sex)[a]	Total
Blank	9	0.0 ± 0.0b	0.0 ± 0.0b	-	0.0 ± 0.0b
UV	9	1.3 ± 0.6b	0.8 ± 0.4a	0.4137	2.1 ± 0.9b
ZETA only	9	9.8 ± 2.5a	0.6 ± 0.3ab	0.0056	10.3 ± 2.6a
UV + ZETA	9	11.2 ± 3.7a	0.9 ± 0.3a	0.0132	12.1 ± 3.9a

[†]Means followed by the same lowercase letter within a column are not significantly different ($P < 0.05$)
[a]Pairwise probabilities for differences between sexes were computed by t-test

Table 3. Mean numbers of moths (± SE) caught in traps baited with UV light alone, food attractant alone, or both[†]

Treatment	*n*	Male	Female	*P* (sex)[a]	Total
Blank	8	0.1 ± 0.1b	0.0 ± 0.0b	0.3506	0.1 ± 0.1c
UV	8	3.3 ± 1.2a	0.5 ± 0.3b	0.0254	3.8 ± 1.4b
Attractant only	8	3.6 ± 1.3a	5.4 ± 1.8a	0.4674	9.0 ± 2.6a
UV + Attractant	8	5.0 ± 1.3a	3.3 ± 0.8a	0.3318	8.3 ± 1.8ab

[†]Means followed by the same lowercase letter within a column are not significantly different ($P < 0.05$)
[a]Pairwise probabilities for differences between sexes were computed by t-test

Figure Legends

Fig. 1. Floor plan of the room where combinatorial experiments were conducted. Asterisks represent the locations of experimental replicates. Shaded areas are the unusable spaces of the experimental arena because of the presence of machinery/electrical wirings and circuit boards. Short, thick lines are the entrance doors. Figure not drawn to scale.

Fig. 2. Spatial distribution and trap captures of *P. interpunctella* males in response to green, UV, and white lights. The data presented are mean + S. E. Bars followed by the same uppercase (black bars) letter or lowercase (white bars) letter are not significantly different ($P < 0.05$). Asterisks over the bars represent significant differences between the light treatment and control (ns = not significant; *, **, *** = significance at 5%, 1%, and 0.1 %, respectively).

Fig. 3. Responses of unmated females to green, UV, and white light emitting diodes in small metal sheds. Actual means + S. E. are presented. Bars with the same uppercase letter or lowercase letter are not significantly different at $P < 0.05$. Asterisks over bars denote statistical differences between the light treatment versus control (ns = not significant; *, **, *** = significance at 5%, 1%, and 0.1 %, respectively).

Fig. 4. Percentage distribution of mated females and their trap captures in green-, UV-. and white-light traps (mean + S.E). Bars followed by the same uppercase letter or lowercase letter are not significantly different at $P < 0.05$. Asterisks represent statistical differences between the light treatment and control (ns = not significant; *, **, *** = significance at 5%, 1%, and 0.1 %, respectively).

Fig. 5. Trap captures (mean + S. E) of *P. interpunctella* adults in traps baited with green light alone, ZETA alone, or both. Bars with the same lowercase letter are not significantly different ($P < 0.05$).

Fig. 6. Oviposition of *P. interpunctella* females in response to different durations of light. Bars with the same lowercase letter are not significantly different ($P < 0.05$).

Fig. 7. Oviposition of *P. interpunctella* females in response to reduced light intensity (8-40 lux) during the scotophase.

Fig. 8. Ovipositional responses of *P. interpunctella* females to reduced scotophase light intensity (>0 - < 8 lux). Bars with the same lowercase letter are not significantly different ($P < 0.05$)

Fig. 1.

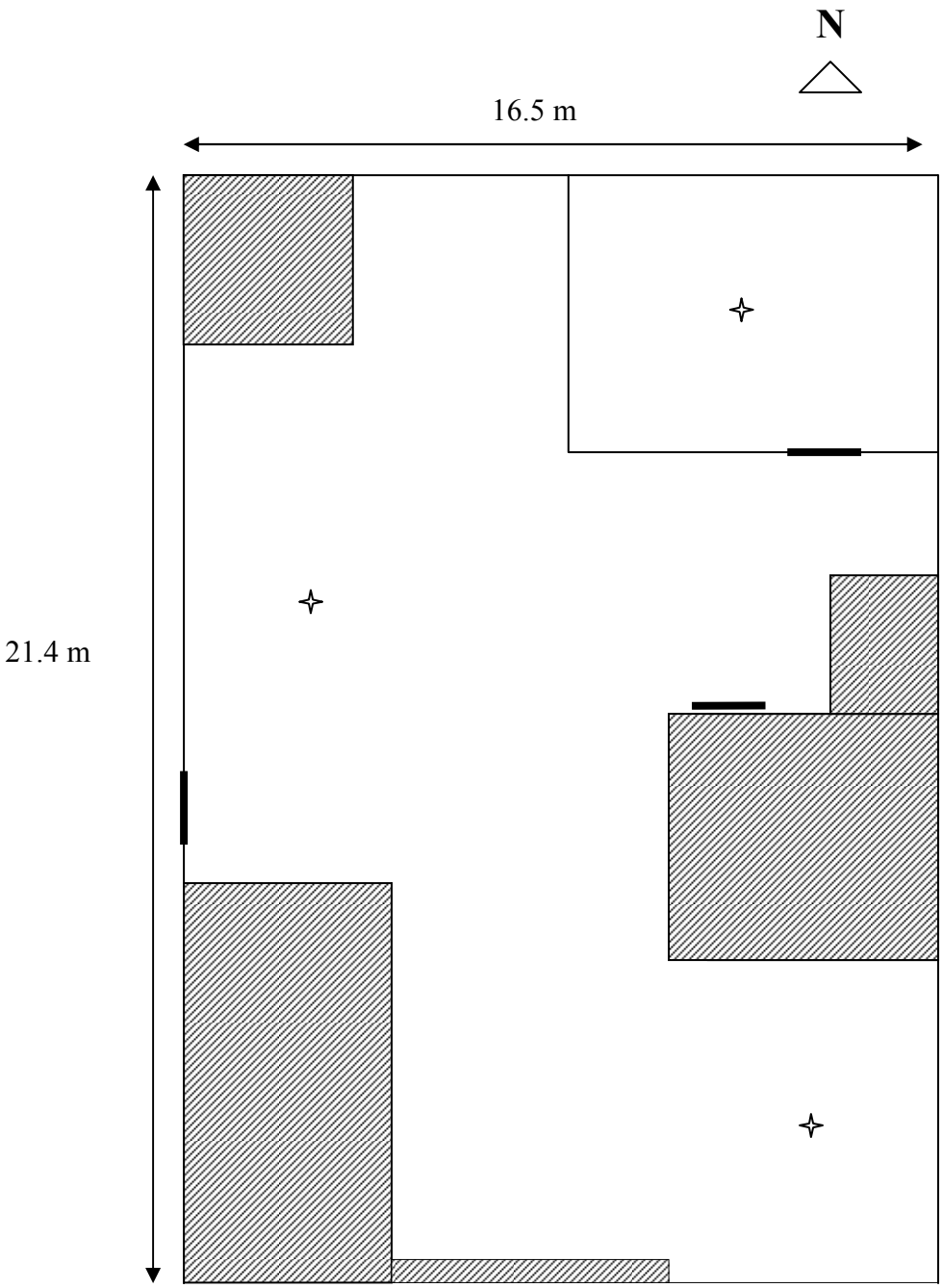


Fig. 2.

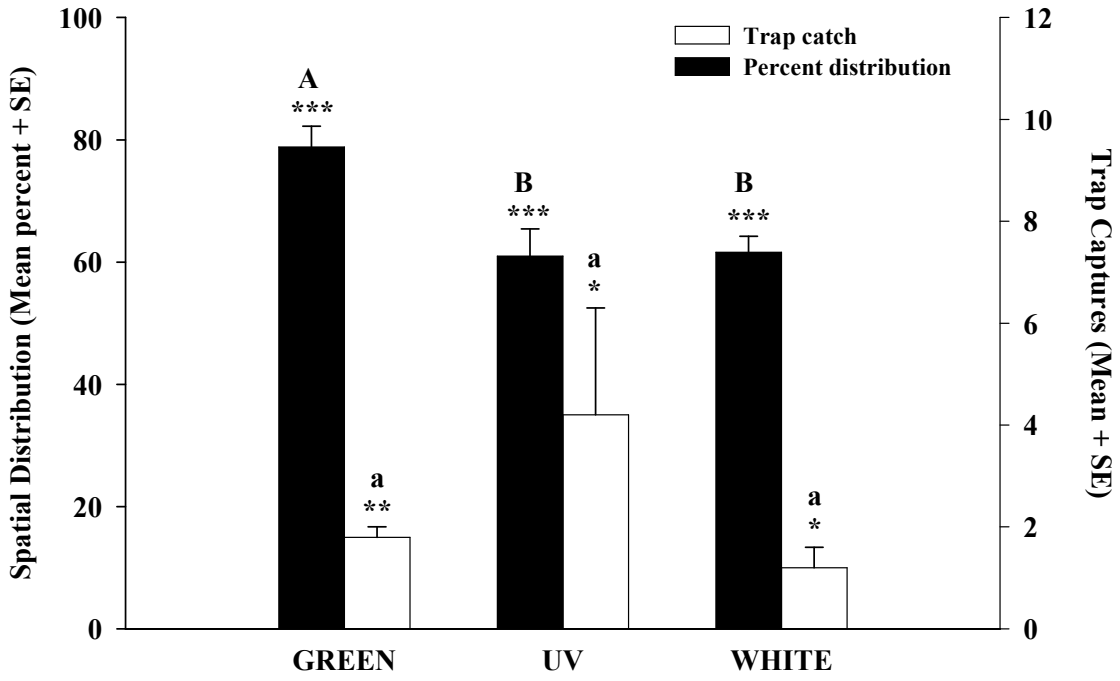

Trap catch
Percent distribution
Spatial Distribution (Mean percent + SE)
Trap Captures (Mean + SE)
100
80
60
40
20
0
12
10
8
6
4
2
0
A
***
a
**
B
***
a
*
B
***
a
*
GREEN
UV
WHITE

Fig. 3.

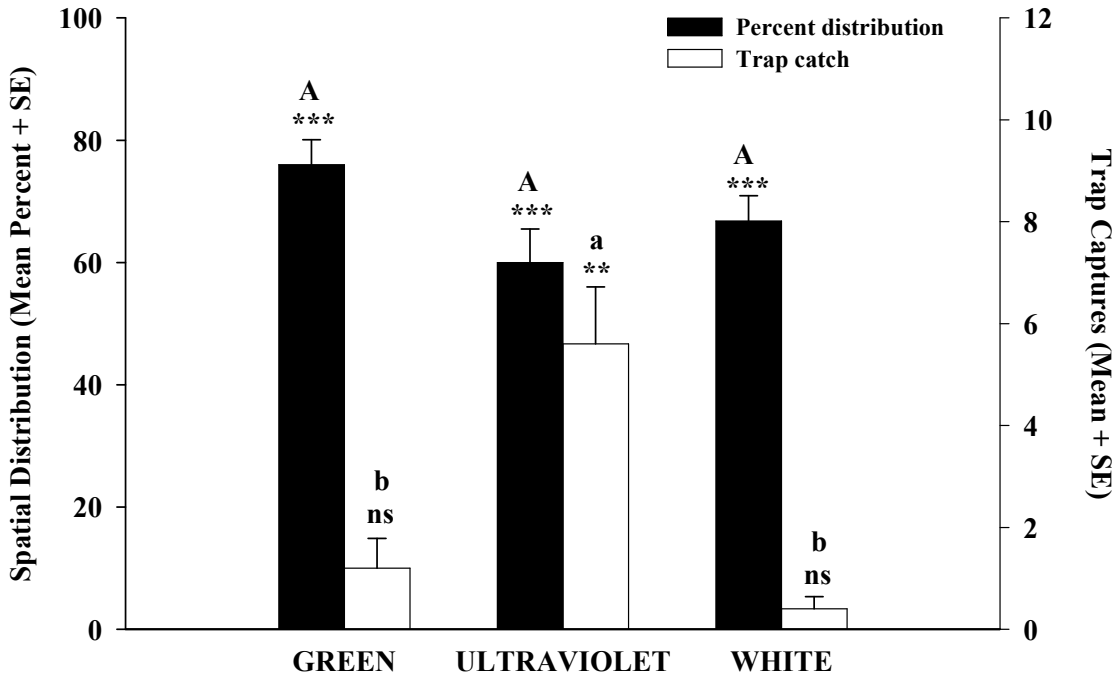

Percent distribution
Trap catch
Spatial Distribution (Mean Percent + SE)
Trap Captures (Mean + SE)
100
80
60
40
20
0
12
10
8
6
4
2
0
A
***
b
ns
A
***
a
**
A
***
b
ns
GREEN
ULTRAVIOLET
WHITE

Fig. 4.

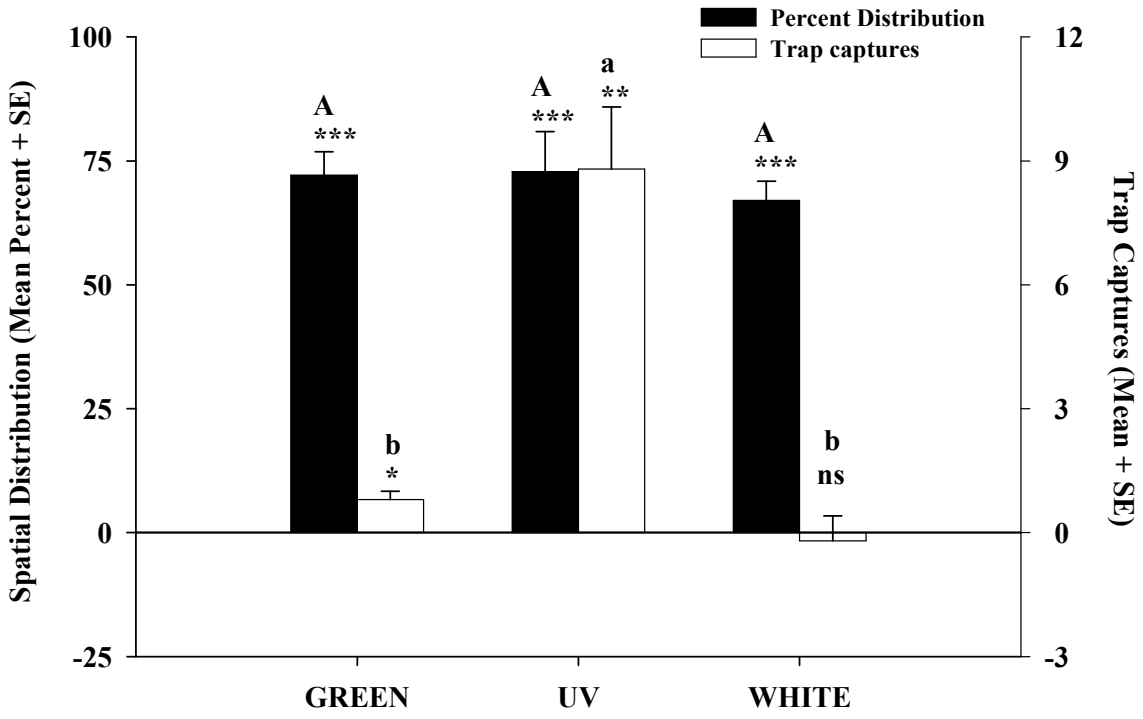

Percent Distribution
Trap captures
Spatial Distribution (Mean Percent + SE)
Trap Captures (Mean + SE)
100
75
50
25
0
-25
12
9
6
3
0
-3
A
***
b
*
A
***
a
**
A
***
b
ns
GREEN
UV
WHITE

Fig. 5.

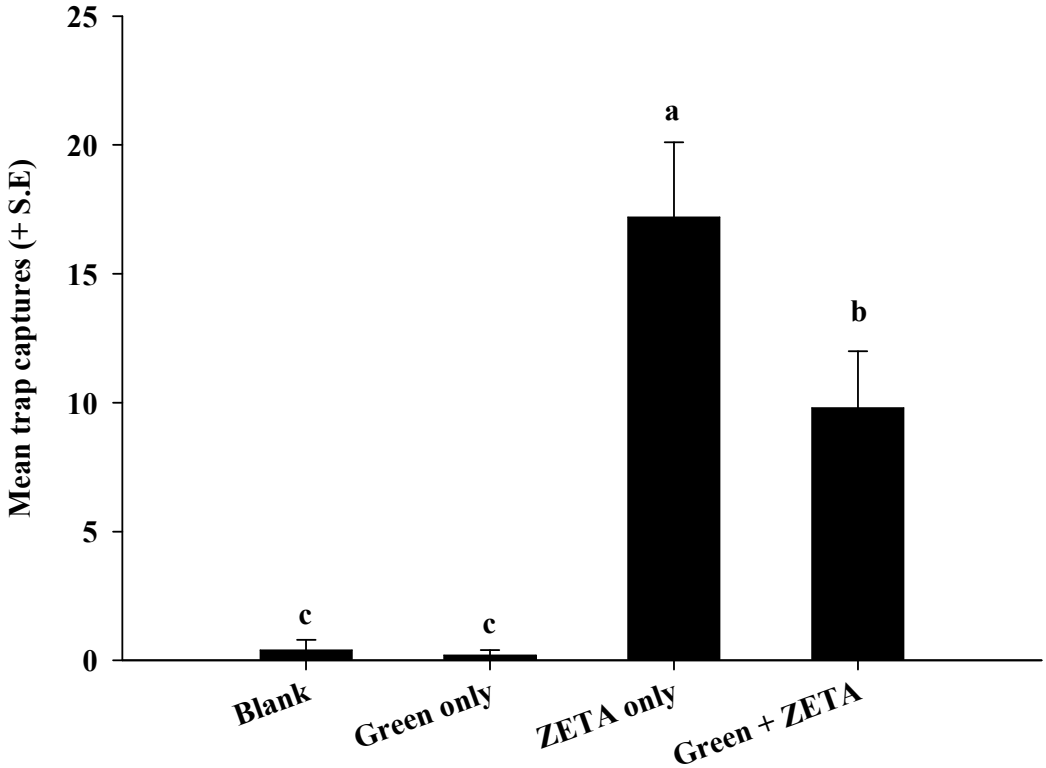

Mean trap captures (+ S.E)
25
20
15
10
5
0
a
b
c
c
Blank
Green only
ZETA only
Green + ZETA

Fig. 6.

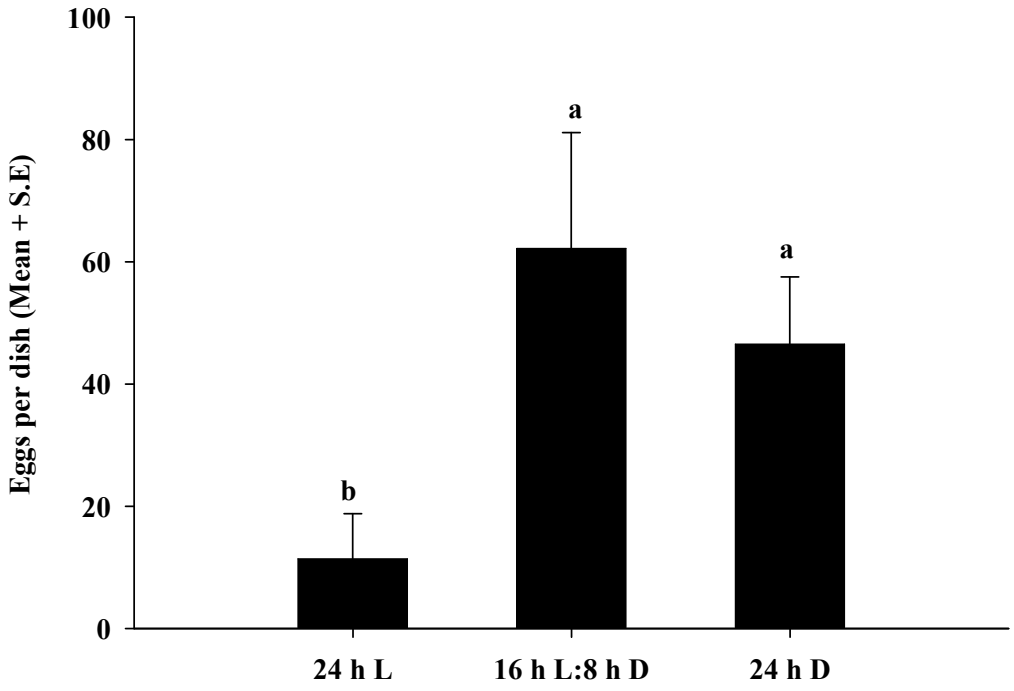


Fig. 7.

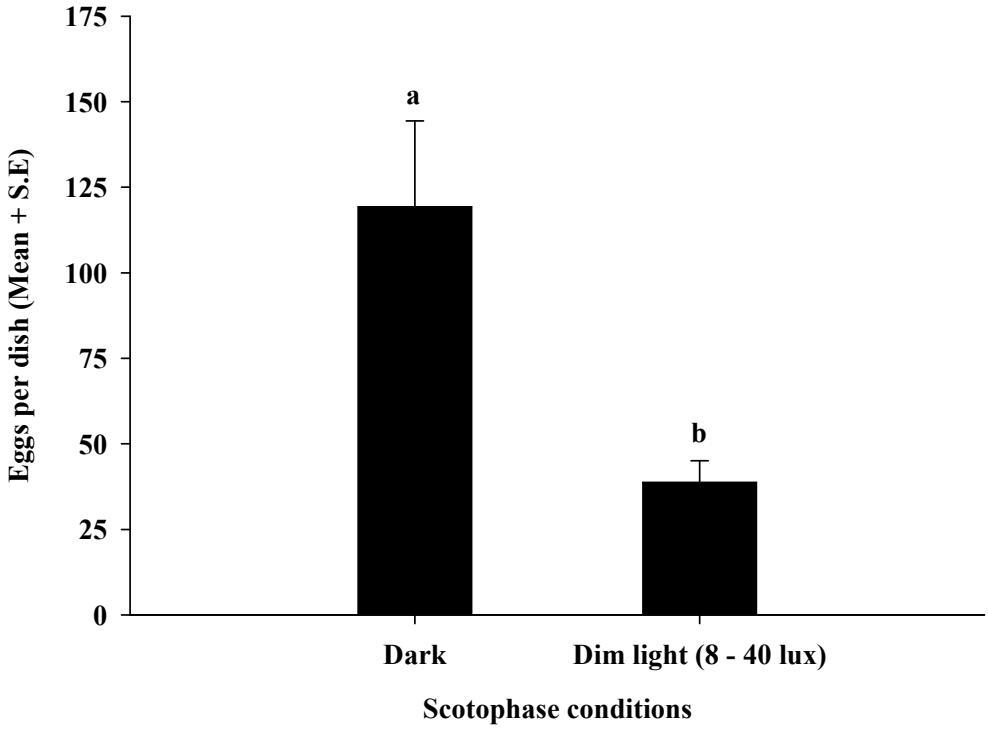
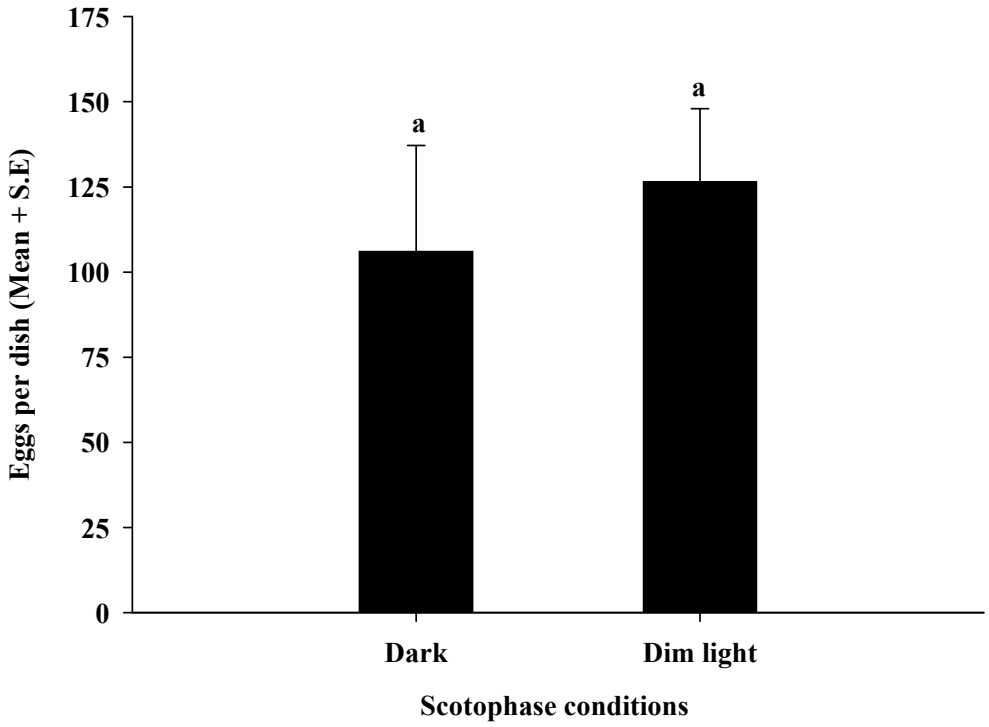

175
150
125
100
75
50
25
0
Eggs per dish (Mean + S.E)
a
b
Dark
Dim light (8 - 40 lux)
Scotophase conditions

Fig. 8.


175
150
125
100
75
50
25
0
Eggs per dish (Mean + S.E)
a
a
Dark
Dim light
Scotophase conditions

CHAPTER V

SUMMARY

Semiochemical-based pest management offers a 'reduced risk' approach in dealing with problematic storage pests (Phillips 1997, 2006). Semiochemicals are chemicals that mediate intraspecific and/or interspecific interactions, and include pheromones and food attractants. In order to effectively manage *P. interpunctella* populations using semiochemicals, a greater emphasis on the study of ecology and behavior of the pest is needed. Although there has been considerable research on the pheromone responses of *P. interpunctella* (reviewed in Phillips 1997 and Mohandass et al. 2007), only recently has the importance of females been recognized and research initiated to study behavioral responses of *P. interpunctella* females to food-based attractants (Nansen and Phillips 2003, Nansen and Phillips 2006, Olsson et al. 2005a, Olsson et al. 2005b, Olsson et al. 2006). A greater understanding of basic female behavior, in addition to studies for enhancing the attraction of males and females to attractant-baited traps, can provide comprehensive tools for future management of *P. interpunctella* populations.

Objectives: Three comprehensive studies were conducted as part of this dissertation that include: 1) close-range oviposition behavior of *P. interpunctella* females to oviposition-stimulating semiochemicals on substrates that vary in texture, number, size, surface area, and shape, 2) oviposition behavior of a laboratory and field populations of *P. interpunctella* in relation to their offspring performance on eleven diets, and 3) responses of *P. interpunctella* adults to light alone and to a combination of light and semiochemicals.

Results: Both semiochemical and physical cues were required to elicit maximum ovipositional responses from *P. interpunctella*. Substrates that offer three dimensional

physical stimuli were preferred compared to substrates that were rough and/or that did not offer raised thigmotactic stimuli. Female oviposition reached a peak when offered certain number of spherical substrates in a bioassay, and oviposition did not increase thereafter. Size of the substrates, rather than the total substrate surface area, determined oviposition response by *P. interpunctella*. Smooth, round substrates were preferred by females compared to flat, angular substrates. Although the studies were conducted in small plastic boxes that prevented interactions with other competing organisms, these findings clearly explain the importance of proximate substrate cues in influencing the oviposition decisions by *P. interpunctella*.

Larvae of a laboratory population and a recent field-collected population of *P. interpunctella* did not survive on walnut, pecan, coriander, and fennel, probably due to the development of rancidity during grinding (walnut, pecan) and/or the presence of toxic chemicals in some of these materials (e.g., coriander, fennel) released upon grinding. Prunes and barley were poor foods for the development of larvae, which was evident from their longer development times. Laboratory larvae, presumably because of their adaptation to laboratory rearing practices, weighed more than the field moths after developing on the same foods under the same conditions. Laboratory adults were heavier on chick pea, lab diet, and soybean. In the case of field moths, soybean and chick pea produced heavier adults. The following conclusions were drawn from the ovipositional host preference experiments: 1) both laboratory and field females will lay eggs in diets unsuitable for their progeny survival in no-choice situations when suitable larval hosts are not available, 2) field moths are more selective in choosing hosts for oviposition than laboratory moths, and 3) adult oviposition preferences correlate with larval performances

in the case of field moths, but this is not the case for the laboratory moths. An indirect, but important conclusion of this experiment was that continuous culturing of laboratory moths for several years may lead to dilution of their "wild" behavior presumably because of genetic alterations that result in behavioral changes.

Spatial distribution and trap captures were influenced by light quality. Ultraviolet (UV) light was more attractive to *P. interpunctella* adults compared to green or white lights. This study clearly showed the importance of reflected light in positive photo-orientation of *P. interpunctella* adults. In small sheds, adult moths were attracted to green, UV, and white light illuminated regions than to the corresponding dark regions. Illuminating an attractant (pheromone/food lure) baited trap with green or UV light or placing a UV light source at the attractant-baited trap did not substantially increase trap captures of *P. interpunctella* when compared to the attractant alone. Presence of a powerful attractant seems to nullify the attractiveness of UV light for adult moths. Oviposition experiments prove that 24 h light inhibits oviposition, and a certain period of darkness is required for females to elicit oviposition. A threshold scotophase light intensity of 8 lux exists for females that when exceeded inhibits oviposition.

Implications: Although close-range oviposition studies involving different substrates may have no immediate 'in field' application, a greater understanding of the female oviposition behavior may lead to more applied research that could provide additional tools for future pest suppression methods. The preference-performance study points out important behavioral differences between field and laboratory populations. Those experiments emphasize the need to realize laboratory colonies of *P. interpunctella* are adapted to the laboratory rearing habitat, and that behavioral studies may require that

researchers introduce field populations at regular intervals into laboratory cultures. Testing the behavioral similarity of older laboratory populations with newly collected field moths can reveal interesting results as done here, and as found with other insects (e.g. the boll weevil, Agee 1986). An outcome of practical significance from the light study in this dissertation is the non-viability of combining a strong attractant with UV or green light. Moreover, because the females require a certain interval of darkness during a 24 h period to oviposit, disrupting their circadian rhythm by maintaining 24 h light in food storage areas could potentially reduce *P. interpunctella* populations. Another option would be to reduce light levels up to 8 lux so that oviposition by females is inhibited.

Future Research: A thorough knowledge of the nutritional and behavioral ecology of an insect pest is an essential prerequisite for developing successful management strategies. Therefore, future studies on *P. interpunctella* should concentrate on 1) identifying the distribution of sensory receptors involved in oviposition on an adult female, 2) understanding the visual ecology of *P. interpunctella* adults, 3) identifying the genetic differences between different field populations of *P. interpunctella*, 4) evaluating the genetic and behavioral changes after successive generations of captive rearing of wild populations, 5) assessing the horizontal and vertical dispersal distances of females for oviposition, and 6) identifying repellant/antifeedant compounds from foods unsuitable for *P. interpunctella* survival.

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VITA

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Doctor of Philosophy

Dissertation: STUDIES ON FACTORS AFFECTING BEHAVIOR, ECOLOGY, AND REPRODUCTIVE SUCCESS OF THE INDIANMEAL MOTH, *PLODIA INTERPUNCTELLA* (HÜBNER) (LEPIDOPTERA: PYRALIDAE)

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Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Dissertation: STUDIES ON FACTORS AFFECTING BEHAVIOR, ECOLOGY, AND REPRODUCTIVE SUCCESS OF THE INDIANMEAL MOTH, *PLODIA INTERPUNCTELLA* (HÜBNER) (LEPIDOPTERA: PYRALIDAE)

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Major: Entomology

Scope and Method of Study: Responses of adult Indianmeal moths to various factors were studied in laboratory and simulated field conditions. Experiments assessed: 1) responses of gravid females to, substrates offering only physical stimuli or both physical and chemical stimuli, and wheat, *Triticum aestivum* L., extract-treated artificial substrates based on texture, number, size, surface area, and shape in 5.7 L plastic boxes under laboratory conditions, 2) correspondence of ovipositional host preferences of two Indianmeal moth populations to progeny survival based on their larval performances on eleven hosts in the laboratory, and 3) behavioral responses of adult Indianmeal moths, to light alone in small metal sheds, and to combinations of light and semiochemicals in a larger experimental arena.

Findings and Conclusions: Experiments conducted in small plastic boxes revealed that female Indianmeal moth respond to substrates that offer both physical and chemical stimuli, and the presence of either stimulus alone did not fully elicit the moths to lay maximum eggs. Substrates offering smooth, round textures received greater numbers of eggs, and glass beads 3-6 mm in size were preferred. Oviposition responses of the gravid females reached a peak when 150 or more extract-treated beads were used. Raised, smooth glass beads were preferred to flat substrates. In the second experiment, significant differences in larval development parameters were observed between the two populations on the eleven hosts. Ovipositional preferences of field-collected moths corresponded with their larval performances, which was not the case with moths from a long-term laboratory colony. Adult Indianmeal moths responded to ultraviolet (UV), green or white lights by orienting to areas illuminated by these lights compared to dark. However, trap captures of adult moths were always higher in UV light traps. When green or UV light was combined with semiochemical(s), no significant increases in trap captures occurred. Attraction of adult moths of either sex to UV light was clearly affected by the presence of a strong attractant. Oviposition experiments found that 24 h of continuous light inhibits oviposition and that a light intensity above 8 lux during the 'dark' phase of a light:dark cycle also inhibits oviposition.

Advisor's Approval: Thomas W. Phillips