



PERGAMON

Journal of Stored Products Research 39 (2003) 53–63

Journal of
**STORED
PRODUCTS
RESEARCH**

www.elsevier.com/locate/jSpr

Effects of delayed mating on reproductive performance of *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae)

Fangneng Huang, Bhadriraju Subramanyam*

Department of Grain Science and Industry, Kansas State University, 201 Shellenberger Hall,
Manhattan, KS 66506-2201, USA

Accepted 8 January 2002

Abstract

Virgin male and female Indianmeal moths, *Plodia interpunctella* (Hübner), were mated soon after emergence or delayed from mating for 1–5 d, to determine the effect of age at mating on the number of spermatophores transferred by males to females, number of eggs laid (fecundity), egg viability, and adult longevity. When male and female moths were mated without delay, all females mated successfully. On average, each mated female had 2.2 spermatophores and laid 161 eggs. About 99% of the eggs laid were viable. Fecundity and egg viability were significantly and positively correlated with the number of spermatophores/female. For each day that mating of virgin male or female *P. interpunctella* was delayed, fecundity decreased by about 25 eggs. Egg viability decreased by 22%/d only when females were delayed from mating. Males delayed from mating for 5 d were unable to inseminate females. However, about 23% of females had one spermatophore when females or both males and females were delayed from mating for 5 d. On average, 22–39 non-viable eggs were laid by a female in treatments where male or female moths were delayed from mating for 5 d. Similarly, unmated (virgin) females laid 33 non-viable eggs. These results suggest that methods that can delay and disrupt mating may be effective behavioral strategies for managing this important pest of stored commodities and processed foods. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Indianmeal moth; Mating delay; Egg production; Egg viability

1. Introduction

Delaying mating has been shown to have a significant effect on the number of spermatophores transferred by males to females, number of eggs laid (fecundity), and egg viability in insect pests belonging to several families of Lepidoptera (Kehat and Gordon, 1977; Ellis and Steele, 1982;

*Corresponding author. Tel.: +1-785-532-4092; fax: +1-785-532-7010.

E-mail address: bhs@wheat.ksu.edu (B. Subramanyam).

Henneberry and Clayton, 1985; Lingren et al., 1988; Wakamura, 1990; Unnithan and Payne, 1991; Walker, 1991; Proshold, 1996; Knight, 1997; Spurgeon et al., 1997; Fadamiro and Baker, 1999). The effects of delayed mating on reproductive performance of stored-product moths have not been extensively investigated. To our knowledge, there is only one paper (Mbata, 1985) that briefly described the effects of delaying female mating on oviposition in the Indianmeal moth, *Plodia interpunctella* (Hübner), an important pest of raw and processed cereals worldwide (Sinha and Watters, 1985).

In the present investigation, we examined in detail the effect of male, female, and both male and female age at mating on the number of spermatophores transferred to females, fecundity, egg viability, and adult longevity. This information will be useful in developing mating disruption strategies using pheromones (Jones, 1988a, b; Knight, 1997) and ultrasound (Acharya and McNeil, 1998) for suppressing *P. interpunctella* populations.

2. Materials and methods

2.1. Insects

Cultures of *P. interpunctella* were reared on a poultry-mash diet (Subramanyam and Cutkomp, 1987) at 28°C, 65% r.h., and 14 h light:10 h dark cycle. The diet (200 g) in 0.95-l glass jars was seeded with approximately 200 eggs. Corrugated paper spools, placed above the diet in each jar, served as pupation sites for wandering larvae. Pupae collected from spools were sexed using characters described by Butt and Cantu (1962). Male and female pupae were placed in separate 0.95-l jars. Jars were checked twice daily, and moths (0–12-h-old) that emerged were used in experiments.

2.2. Mating treatments

There were a total of 18 mating treatments (see Table 1). Newly emerged virgin females were paired with newly emerged virgin males or with 1–5-d-old virgin males (treatments 1–6). Newly emerged virgin males were paired with 1–5-d-old virgin females (treatments 7–11), and 1–5-d-old virgin females were mated with virgin males of the same age (treatments 12–16). In each of these treatments, five females were paired with five males. In two of the treatments, five newly emerged virgin females were not paired with males (treatment 17), and five newly emerged virgin males were not paired with females (treatment 18).

Each treatment was replicated 3–6 times by introducing the appropriate number of moths in 0.95-l glass jars. After moth introduction, jars were covered with wire mesh screens (1.58 mm² holes) fitted to metal lids. The jars were inverted over 9-cm diameter glass Petri dishes to collect the eggs that dropped through the mesh. All jars were held in the same growth chamber used for rearing the insects. Petri dishes and jars were checked daily between 8:00 a.m. and 12:00 noon local time, to count the number of eggs laid and number of dead moths. Jars were checked until all adults were dead.

Eggs collected daily were placed in 25 mm diameter × 10 mm high plastic Petri dishes. These dishes were placed above 10 g of *P. interpunctella* rearing diet held in 0.47-l glass jars, so that

Table 1

Effects of delayed mating by male, female, or both male and female *Plodia interpunctella* on preoviposition period and spermatophore transfer

Treatment no.	Treatment		Preoviposition period (d) (Mean ± SE) ^a	No. females dissected	No. spermatophores/ female (Mean ± SE) ^a	Percentage of females with 0–4 spermatophores/female				
	Female age (d)	Male age (d)				0	1	2	3	4
1 ^b	0	0	0.67 ± 0.21b	16	2.24 ± 0.12a	0.0	6.3	62.5	31.3	0.0
2 ^c	0	1	1.00 ± 0.26b	29	1.83 ± 0.19ab	0.0	34.5	44.8	20.7	0.0
3 ^c	0	2	0.33 ± 0.21b	30	1.57 ± 0.29bc	0.0	60.0	26.7	10.0	3.3
4 ^b	0	3	0.50 ± 0.29b	20	0.85 ± 0.05ef	15.0	85.0	0.0	0.0	0.0
5 ^d	0	4	1.00 ± 0.00b	24	0.62 ± 0.17efg	37.5	62.5	0.0	0.0	0.0
6 ^c	0	5	2.67 ± 0.42a	30	0.00 ± 0.00i	100.0	0.0	0.0	0.0	0.0
7 ^c	1	0	1.50 ± 0.22	30	1.73 ± 0.15bc	0.0	46.7	36.7	16.7	0.0
8 ^c	2	0	2.17 ± 0.17	29	1.40 ± 0.25cd	3.4	69.0	13.8	10.3	3.4
9 ^c	3	0	3.00 ± 0.00	30	1.03 ± 0.06de	6.7	86.7	6.7	0.0	0.0
10 ^c	4	0	4.00 ± 0.00	29	0.52 ± 0.07fgh	55.2	34.5	10.3	0.0	0.0
11 ^c	5	0	5.00 ± 0.00	30	0.20 ± 0.07hi	76.7	23.3	0.0	0.0	0.0
12 ^e	1	1	1.00 ± 0.00	15	1.80 ± 0.12abc	0.0	33.3	53.3	13.3	0.0
13 ^e	2	2	2.00 ± 0.00	15	1.07 ± 0.07de	0.0	93.3	6.7	0.0	0.0
14 ^d	3	3	3.00 ± 0.00	21	0.85 ± 0.05ef	14.3	85.7	0.0	0.0	0.0
15 ^c	4	4	4.00 ± 0.00	30	0.33 ± 0.07ghi	66.7	33.3	0.0	0.0	0.0
16 ^c	5	5	5.00 ± 0.00	30	0.03 ± 0.03i	76.7	23.3	0.0	0.0	0.0
17 ^c		female	2.17 ± 0.54a							

^a Means in a single column followed by different letters are significantly different ($P < 0.05$; least squares means test).

^b $n = 4$ replications.

^c $n = 6$ replications.

^d $n = 5$ replications.

^e $n = 3$ replications.

larvae hatching from eggs could infest the diet. These jars were held at the same environmental conditions mentioned above. After 1 week, dishes were checked for eggs that failed to hatch. Egg viability in each dish was determined from the number of eggs out of the total that hatched. Dead female moths were collected and preserved in vials containing 100% ethanol. Females were dissected under the stereomicroscope to determine the number of spermatophores in the bursa copulatrix (Lum, 1979).

2.3. Data analysis

A completely random design was used for the experiments. Only the percentage of egg viability data were transformed to angular values (Zar, 1984) before analysis to stabilize variances across the treatments. Data on the number of spermatophores transferred to females, preoviposition period, number of eggs laid, egg viability, or adult (male or female) longevity were subjected to one-way analysis of variance using the PROC GLM procedure (SAS Institute, 1990), to determine treatment differences. Treatment means were separated using the least squares means test at the

$\alpha = 0.05$ level (SAS Institute, 1990). For each treatment, the frequency distribution of females with 0–4 spermatophores was expressed as a percentage of the total females dissected. Linear regressions (SAS Institute, 1990) were used to determine the relationship between mating delay (in days) and each of the biological responses observed, and between any two biological responses.

3. Results

3.1. Effects of delayed mating on preoviposition period

Preoviposition data in treatments where female mating was delayed were not subjected to statistical analysis, because the preoviposition period was confounded with the number of days females were delayed. Comparisons among treatments 1–6 and 17 (Table 1) showed significant differences ($F = 7.28$; $df = 6, 32$; $P = 0.0001$). The preoviposition period was about 2–3 d in virgin females or males delayed from mating for 5 d. In treatments where males were delayed by 0–4 d, females laid eggs within 1 d, and these treatments were not significantly different from one another ($P > 0.05$). In treatments where mating by females was delayed (treatments 7–16), eggs also were laid within a day.

3.2. Effects of delayed mating on spermatophore transfer

The number of spermatophores obtained per female varied significantly among the treatments ($F = 21.45$; $df = 15, 66$; $P = 0.0001$). The highest mean number of spermatophores (2.24/female) was observed when males and females were paired without delay (treatment 1) (Table 1). In this treatment, about 63% of females had two spermatophores while 31% had three spermatophores. The number of spermatophores per female decreased significantly when mating by males, females, or both sexes was delayed. Spermatophore transfer did not occur when 5-d-old males mated with 0-d-old females (treatment 5). Generally, 0–3 spermatophores were found in females, and the maximum number observed was four in two treatments (treatments 3 and 8). The frequency distribution of spermatophores also varied among the treatments. All females had at least one spermatophore if mating delay by males, females, or both was ≤ 1 d.

The number of spermatophores per female decreased ($P < 0.01$) as a function of male delay ($Y = 2.30 - 0.44X$; $n = 6$; $R^2 = 0.983$), female delay ($Y = 2.15 - 0.32X$; $n = 6$; $R^2 = 0.749$), or both male and female delay ($Y = 2.17 - 0.45X$; $n = 6$; $R^2 = 0.982$).

3.3. Effects of delayed mating on fecundity

Fecundity was different among treatments 1–17 ($F = 36.08$; $df = 16, 85$; $P = 0.0001$). More eggs were laid when there was no mating delay (treatment 1) than in any other treatment combination (Table 2). Virgin females laid about 33 eggs. In treatments where females, males, or both sexes were delayed by 5 d, fecundity was not significantly different ($P > 0.05$).

There was a positive relationship ($P < 0.01$) between fecundity and number of spermatophores per female ($Y = 18.59 + 55.72X$; $n = 6$; $R^2 = 0.941$). Fecundity decreased ($P < 0.01$) as a function

Table 2

Effect of delayed mating on fecundity, egg viability, and adult longevity of *Plodia interpunctella*

Treatment no.	Treatment		Mean \pm SE ^a			
	Female age (d)	Male age (d)	No. eggs/female	Egg viability (%)	Male longevity (d)	Female longevity (d)
1	0	0	161.3 \pm 15.4a	99.2 \pm 0.3a	4.2 \pm 0.3e	5.3 \pm 0.4efg
2	0	1	120.3 \pm 9.4b	99.4 \pm 0.4a	4.9 \pm 0.1de	6.1 \pm 0.3abcde
3	0	2	115.9 \pm 16.9b	99.1 \pm 4.9abc	4.9 \pm 0.2de	5.0 \pm 0.5fg
4	0	3	72.9 \pm 7.9c	86.7 \pm 9.3abc	5.4 \pm 0.1bcd	4.7 \pm 0.2g
5	0	4	57.7 \pm 11.0cde	92.1 \pm 6.7ab	6.5 \pm 0.3a	5.9 \pm 0.3abcde
6	0	5	22.4 \pm 4.7f	0.0 \pm 0.0f	6.2 \pm 0.1ab	6.7 \pm 0.3a
7	1	0	107.4 \pm 14.7b	96.3 \pm 1.5ab	5.6 \pm 0.4bcd	6.2 \pm 0.2abcd
8	2	0	78.1 \pm 8.2c	90.8 \pm 2.7bc	5.6 \pm 0.3bc	6.5 \pm 0.3ab
9	3	0	71.9 \pm 7.6c	73.4 \pm 5.8de	5.9 \pm 0.4ab	6.3 \pm 0.2abc
10	4	0	30.9 \pm 4.6ef	6.8 \pm 5.9f	6.0 \pm 0.4ab	6.6 \pm 0.2a
11	5	0	38.5 \pm 7.2def	0.0 \pm 0.0f	5.8 \pm 0.4abc	6.6 \pm 0.2a
12	1	1	116.9 \pm 16.5b	98.1 \pm 0.6ab	4.9 \pm 0.5cde	5.4 \pm 0.3defg
13	2	2	68.3 \pm 10.1c	83.4 \pm 5.5cd	4.8 \pm 0.2de	5.3 \pm 0.3efg
14	3	3	66.4 \pm 11.5cd	58.4 \pm 15.1e	5.4 \pm 0.2bcd	5.7 \pm 0.3bcdef
15	4	4	36.9 \pm 3.4ef	18.5 \pm 15.2f	6.0 \pm 0.3ab	6.3 \pm 0.2abcd
16	5	5	27.1 \pm 5.4f	0.0 \pm 0.0f	6.0 \pm 0.0ab	6.4 \pm 0.1ab
17	female		32.5 \pm 5.9ef	0.0 \pm 0.0f		5.6 \pm 0.3cdef
18		male			5.7 \pm 0.2bc	

^a Means within each column followed by different letters are significantly different ($P < 0.05$; least squares means test).

of male delay ($Y = 157.84 - 26.44X$; $n = 6$; $R^2 = 0.974$), female delay ($Y = 142.0 - 24.28X$; $n = 6$; $R^2 = 0.893$), or both male and female delay ($Y = 144.69 - 26.02X$; $n = 6$; $R^2 = 0.92$).

To show shifts in oviposition as a function of male age at mating, the mean daily oviposition data were plotted over a 9-d period using data from treatments 1–6 and 17 (Fig. 1). In all seven treatments, very few or no eggs were laid during the first day. When newly emerged females were mated with newly emerged or 1-d-old males, most of the eggs (roughly 60%) were laid on the third and fourth day after mating. When newly emerged females were mated with 2–3-d-old males, 52–70% of the eggs were laid on the second and third day after mating. Females mated with 4-d-old males laid about 90% of the eggs between the second and fifth day after mating. Females mated with males delayed by 5 d laid most of the eggs 5 d after mating, and very few eggs were laid on the ninth day after pairing.

3.4. Effects of delayed mating on egg viability

Egg viability varied among the treatments ($F = 36.08$; $df = 16, 85$; $P = 0.0001$). Egg viability among treatments in which 0–4-d-old males were mated with newly emerged females was not different ($P > 0.05$) (Table 2). However, egg viability decreased when females or both males and females were delayed from mating for ≥ 2 d, and the decrease in egg viability as a function of

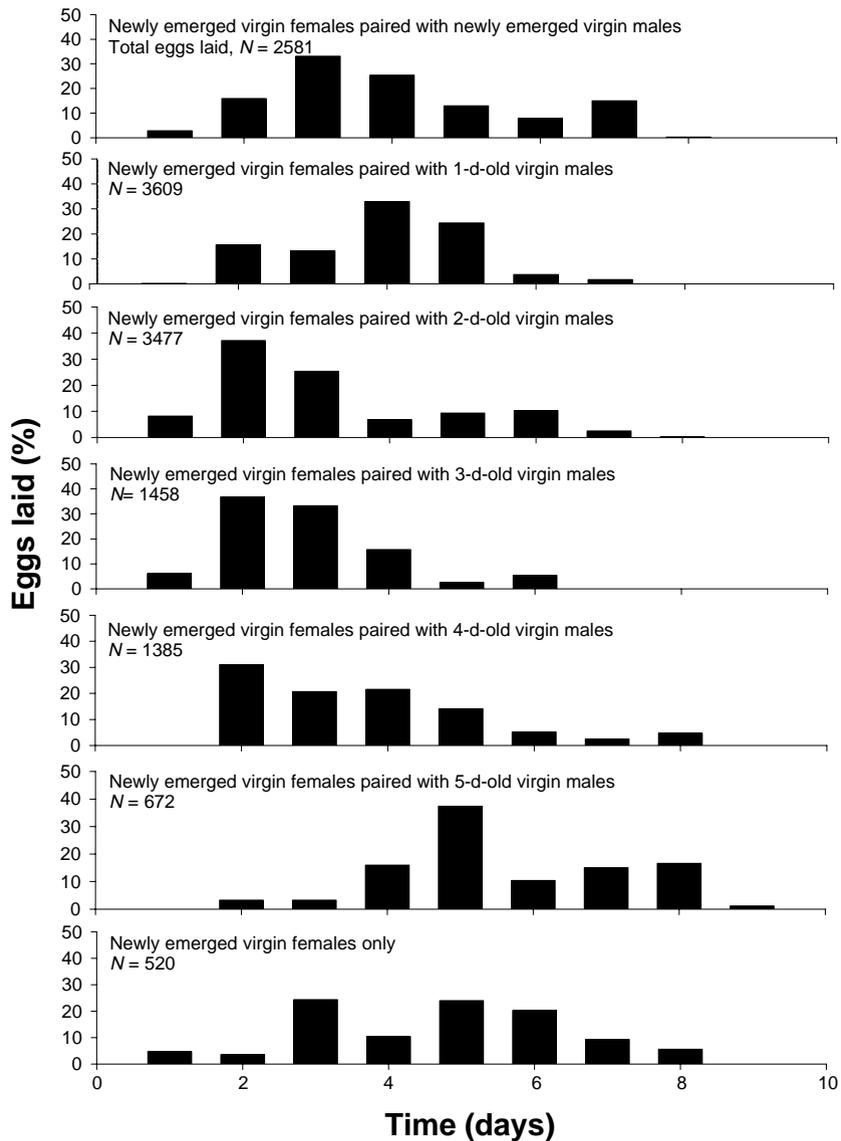


Fig. 1. Daily oviposition patterns of unmated female *Plodia interpunctella* and newly emerged females mated with 0–5 d-old males. For each treatment, total number of eggs laid (N) represents eggs laid by all females.

moth age was greater in these treatments when compared with treatments where only males were delayed from mating. This indicated that egg viability was more closely related to female than male age.

There was a positive relationship ($P < 0.01$) between egg viability and number of spermatophores per female ($Y = 10.86 + 51.55X$; $n = 6$; $R^2 = 0.749$). However, there was no relationship between egg viability and male delay. There was a negative relationship between egg viability and female delay ($Y = 116.9 - 22.3X$; $n = 6$; $R^2 = 0.839$), and male and female delay ($Y = 113.9 - 21.7X$; $n = 6$; $R^2 = 0.931$).

3.5. Effects of delayed mating on adult longevity

Average female longevity among treatments ranged from 5 to 7 d and male longevity from 4 to 7 d (Table 2). A comparison among treatments showed that mating delay had a small, but significant, effect on the longevity of males ($F = 3.81$; $df = 16, 71$; $P = 0.0001$) and females ($F = 4.3$; $df = 16, 71$; $P = 0.0001$). The longevity of both virgin males and females was similar (5.6 d).

Linear regressions indicated a positive relationship ($P < 0.05$) between female longevity (Y) and female delay ($Y = 5.71 + 0.21X$; $n = 6$; $R^2 = 0.661$) or both male and female delay ($Y = 5.12 + 0.25X$; $n = 6$; $R^2 = 0.843$). However, female delay was not linearly related ($P > 0.05$) to male delay. Male longevity was positively related only to male delay ($Y = 4.26 + 0.44X$; $n = 6$; $R^2 = 0.886$).

In general, the adverse effects observed when both male and female *P. interpunctella* were delayed from mating were not additive, and more closely resembled those observed in treatments where only the females were delayed from mating.

4. Discussion

The preoviposition period observed in our study was not affected when males were delayed from mating for 1–4 d. However, the preoviposition period was significantly longer (2.7 d) when males were delayed from mating for 5 d, and the preoviposition period (Table 2) and oviposition patterns (Fig. 1) were similar to those observed with unmated females (treatment 17). In general, there was a negative relationship between preoviposition period and number of spermatophores per female. The preoviposition period of the spiny bollworm, *Earias insulana* Boisduval, also was significantly prolonged in unmated females, enabling the female to delay oviposition until after mating (Kehat and Gordon, 1977).

The presence of a spermatophore in female *P. interpunctella* is indicative of successful mating (Brower, 1975). Brower (1975) paired five newly emerged *P. interpunctella* males with a similar number of newly emerged females and found that 98% of the females had successfully mated, and on average, each female had 2.5 spermatophores. In our study, when five newly emerged male and female *P. interpunctella* were paired without delay, all females mated successfully, and on average, each female had 2.2 spermatophores (Table 1).

Plodia interpunctella fecundity was highest when there was no mating delay (Table 2), and a positive relationship between the number of spermatophores per female and fecundity suggests that multiple mating could increase egg production. Multiple-mated females of the European corn borer, *Ostrinia nubilalis* (Hübner) also deposited a significantly larger portion of their egg complement relative to single-mated or unmated females (Fadamiro and Baker, 1999). Similar positive correlations between mating frequency and egg production were observed in the red bollworm, *Diparopsis castanea* Hampson (Marks, 1976), green-veined white butterfly, *Pieris napi* L. (Wilkund et al., 1993), true armyworm, *Pseudaletia unipuncta* (Hawthorne) (Svärd and McNeil, 1994), cabbage looper, *Trichoplusia ni* (Hübner) (Ward and Landolt, 1995; Landolt, 1997), and spruce budworm, *Choristoneura fumiferana* (Clemens) (Delisle and Hardy, 1997). We do not believe that the number of spermatophores is necessarily related to increased egg production in

P. interpunctella. Brower (1975) reported that the number of times a female mated was not related to the number of eggs laid. Similarly, Steele (1970), using a closely related stored-product moth (almond moth, *Ephestia cautella* (Walker)) reported that the number of eggs laid was similar (389–406) when females mated one to three times. Therefore, oviposition in *P. interpunctella* appears to be stimulated directly or indirectly by the transfer of sperm by males to females (Norris, 1933; Lum and Arbogast, 1980). The increased egg production in multiple-mated females may be due to the transfer of nutrient secretions, pigments, inorganic ions, proteins, juvenile hormones and ecdysteroids by males to females during copulation (Benz, 1969; Henneberry and Clayton, 1984; Park et al., 1998).

We found that for each day mating was delayed, there were 0.32–0.45 fewer spermatophores and 24–26 fewer eggs produced per female. The decreased number of spermatophores with age could be due to fewer successful matings by males or females. In the tobacco budworm, *Heliothis virescens* (F.), male accessory sex gland secretions were essential for spermatophore formation, egg maturation, and fecundity (Ramaswamy et al., 1997; Park et al., 1998). A decrease in the quantity and quality of accessory gland secretions and hormones transferred to females during copulation, or total absence of these secretions (Park et al., 1998), with increasing male *P. interpunctella* age may have resulted in decreased or no spermatophore formation and reduced egg production. Similarly, as female *P. interpunctella* aged, they were perhaps less receptive to males, and this could have resulted in a decrease in the number of spermatophores per female. Furthermore, the decreased number of spermatophores in female *P. interpunctella* that were delayed from mating may be due to the degenerated oocyte relics that prevented male spermatophores from reaching the bursa copulatrix. Lum (1982) reported that newly emerged female *P. interpunctella* that were prevented from mating produced oocyte relics due to oosorption in the bursa seminalis (Lum, 1979). These relics obstructed the sperm translocation when mating eventually occurred (Lum, 1983).

Park et al. (1998) proposed a mechanism by which mating by male *H. virescens* enhances egg production. The male during copulation transfers juvenile hormone, which directly triggers egg production. In addition this hormone also triggers the female's corpora allata to produce more juvenile hormone, consequently resulting in increasing egg production. For females that are delayed from mating, the absence of this paternal investment results in the retention of the unfertilized oocytes, because the female's corpora allata are not triggered to produce and release the necessary juvenile hormone required for oocyte development (Park et al., 1998). Retention of mature oocytes in unmated female *P. interpunctella* was reported by Mbata (1985). He found that the number of oocytes in the ovaries of female *P. interpunctella* that were not delayed or those delayed from mating for 2 or 5 d were similar. Females that were not delayed from mating laid 246 eggs, while those delayed for 2 or 5 d laid 34% or 65% fewer eggs (Mbata, 1985). We found that a 2-d mating delay by females resulted in a 52% decrease in fecundity, while a 5-d delay resulted in a 76% decrease (Table 2). Unmated female *P. interpunctella* in our study laid about 33 eggs, whereas in a study reported by Mbata (1985) unmated females laid about 24 eggs.

The daily oviposition patterns of female *P. interpunctella* (Fig. 1), where males and females were mated without delay or where the male was delayed by 1 d, were comparable to those reported by Mbata (1985). He reported that about 34–58% and 84–97% of the eggs were laid by *P. interpunctella* within 2–4 d after mating, respectively. Quick commencement of mating and shorter preoviposition periods (Mbata, 1986) could have contributed to the early egg laying observed

when 2–4-d-old males were mated with newly emerged females. The oviposition patterns of females mated with 5-d-old males and virgin males were similar, because in both cases, females lacked spermatophores.

Egg viability was affected more by female than male age. Egg viability did not decrease until males were 5-d-old. The 5-d-old males failed to inseminate the females (Table 1). Consequently, sperm were unavailable to fertilize the eggs. The eggs laid by females in this treatment were similar to those laid by virgin females, and in both cases the eggs failed to hatch. As indicated above, mating and transfer of paternal investment is important for egg maturation, oviposition, and egg viability (Henneberry and Clayton, 1984; Ramaswamy et al., 1997; Park et al., 1998). Viability of *P. interpunctella* eggs decreased by 22% for each day female mating was delayed. The decrease in egg viability with female age may be due to eggs not being fertilized. The number of degenerating oocyte relics in unmated females increases with age, and this could have prevented spermatophores from reaching the bursa copulatrix when these females were eventually mated with males (Lum, 1982, 1983). Although data were not collected, some of the eggs that failed to hatch in our experiments were not embryonated. Proshold (1996) observed that embryonation of the gypsy moth, *Lymantria dispar* (L.), eggs decreased with female age, and eggs laid by older females were less viable than those laid by younger females.

Lum and Flaherty (1969) reported that mated *P. interpunctella* moths lived for approximately 5–7 days. The mean adult longevities for mated moths (Table 2) in our study fell within these ranges. The linear relationships we observed between longevity of either male or female and corresponding male, female, or both male and female delay may have been confounded with the days the moths were delayed. For example, in the 5 d delay treatment, it is impossible for moths to have lived for <5 d. Delayed mating by males did not affect female longevity and vice versa. Brower (1975) also did not find any relationship between the number of times a female mated and its longevity. In our study, unmated females lived the same duration as those that mated without any delay, while unmated males lived 1.5 d longer than males that mated without any delay. From a practical standpoint, mating delay did not have a great impact on adult longevity. Similar results between delayed mating and longevity were observed with *L. dispar* (Proshold, 1996), but not with the shoot stem borer, *Chilo partellus* (Swinhoe) (Unnithan and Payne, 1991). Increased female longevity associated with mating delay has been reported in several other species of Lepidoptera (Ellis and Steele, 1982; Proshold et al., 1982; Henneberry and Clayton, 1985; Lingren et al., 1988).

In conclusion, the number of eggs laid and egg viability were significantly reduced when adult male, female, or both male and female *P. interpunctella* were delayed from mating. Delaying females as opposed to males from mating had a greater impact on egg laying and egg viability. These results suggest that techniques such as the use of high-pheromone concentrations (Jones, 1988a, b) or ultrasound (Mullen and Tsao, 1971; Acharya and McNeil, 1998), which can delay or disrupt mating, would be an effective behavioral management strategy to suppress populations of this important stored-product moth.

Acknowledgements

This project was funded by Weitech, Inc., Sisters, Oregon. We are grateful to Jim Campbell (USDA-ARS, GMPRC, Manhattan, Kansas) and Christian Nansen (Oklahoma State University,

Stillwater, Oklahoma) for reviewing the manuscript. This paper is Contribution No. 02-43-J of the Kansas Agricultural Experiment Station, Kansas State University, Manhattan, Kansas.

References

- Acharya, L., McNeil, J.N., 1998. Predation risk and mating behavior: the responses of moths to bat-like ultrasound. *Behavioral Ecology* 9, 552–558.
- Benz, G., 1969. Stimulation of oogenesis in *Pieris brassicae* by juvenile hormone derivative farnesenic acid ethyl ester. *Experientia* 26, 1012.
- Brower, J.H., 1975. *Plodia interpunctella*: effect of sex ratio on reproductivity. *Annals of the Entomological Society of America* 68, 847–851.
- Butt, B.A., Cantu, E., 1962. Sex determination of lepidopterous pupae. Agricultural Research Service Report 33–75, United States Department of Agriculture, pp. 1–7.
- Delisle, J., Hardy, M., 1997. Male larval nutrition influences the reproductive success of both sexes of the spruce budworm *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Functional Ecology* 11, 451–463.
- Ellis, P.E., Steele, G., 1982. Effects of delayed mating on fecundity of females of *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae). *Bulletin of Entomological Research* 72, 295–302.
- Fadamiro, H.Y., Baker, T.K., 1999. Reproductive performance and longevity of female European corn borer, *Ostrinia nubilalis*: effect of multiple mating, delay in mating and adult feeding. *Journal of Insect Physiology* 45, 385–392.
- Henneberry, T.J., Clayton, T.T., 1984. Time of emergence, mating, sperm movement, and transfer of ejaculatory duct secretory fluid by *Heliothis virescens* (F.) (Lepidoptera: Noctuidae) under reversed light–dark cycle laboratory conditions. *Annals of the Entomological Society of America* 77, 301–305.
- Henneberry, T.J., Clayton, T.T., 1985. Tobacco budworm moths (Lepidoptera: Noctuidae): effect of time of emergence, male age, and frequency of mating on sperm transfer and egg viability. *Journal of Economic Entomology* 78, 379–382.
- Jones, O.T., 1988a. Practical applications of pheromones and other semiochemicals. In: Howse, P., Stevens, I., Jones, O. (Eds.), *Insect Pheromones and Their Use in Pest Management*. Chapman & Hall, London, pp. 263–352.
- Jones, O.T., 1988b. The commercial exploitation of pheromones and other semiochemicals. *Pesticide Science* 54, 293–296.
- Kehat, M., Gordon, D., 1977. Mating ability, longevity and fecundity of the spiny bollworm, *Earias insulana* (Lepidoptera: Noctuidae). *Entomologia Experimentalis et Applicata* 22, 688–698.
- Knight, A.L., 1997. Delay of mating of codling moth in pheromone disrupted orchards. In: Witzgall, P., Ar, H. (Eds.), *Technology Transfer in Mating Disruption*. IOBC Bulletin 20, 203–206.
- Landolt, P.J., 1997. Cabbage looper (Lepidoptera: Noctuidae) fecundity maximized by a combination of access to water and food, and remating. *Annals of the Entomological Society of America* 90, 783–789.
- Lingren, P.D., Warner, W.B., Henneberry, T.J., 1988. Influence of delayed mating on egg production, egg viability, mating and longevity of female pink bollworm (Lepidoptera: Gelechiidae). *Environmental Entomology* 17, 86–89.
- Lum, P.T.M., 1979. Degeneration of ova in the bulla seminalis of Lepidoptera. *Journal of Insect Physiology* 25, 595–599.
- Lum, P.T.M., 1982. Degenerating oocytes: a physical barrier to sperm translocation in female *Plodia interpunctella* (Hübner) and *Ephestia cautella* (Walker). *Journal of Georgia Entomological Society* 17, 421–428.
- Lum, P.T.M., 1983. Oocyte degeneration in *Plodia interpunctella* Hübner and *Cadra cautella* (Walker) (Lepidoptera: Pyralidae): influence of temperature and humidity. *Environmental Entomology* 12, 1539–1541.
- Lum, P.T.M., Arbogast, R.T., 1980. Ultrastructure of setae in the spermathecal gland of *Plodia interpunctella* (Lepidoptera: Pyralidae). *International Journal of Insect Morphology and Embryology* 9, 251–253.
- Lum, P.T.M., Flaherty, B.R., 1969. Effect of mating with males reared in continuous light or in light–dark cycles on fecundity in *Plodia interpunctella* (Hübner) (Lepidoptera: Phycitidae). *Journal of Stored Products Research* 5, 89–94.
- Marks, R.J., 1976. Mating behavior and fecundity of the red bollworm *Diparopsis castanea* Hmps. (Lepidoptera: Noctuidae). *Bulletin of Entomological Research* 66, 145–158.

- Mbata, N.G., 1985. Some physical and biological factors affecting oviposition by *Plodia interpunctella* (Hübner) (Lepidoptera: Phycitidae). *Insect Science and its Application* 6, 597–604.
- Mbata, N.G., 1986. Combined effect of temperature and relative humidity on mating activities and commencement of oviposition in *Plodia interpunctella* (Hübner) (Lepidoptera: Phycitidae). *Insect Science and its Application* 7, 623–628.
- Mullen, M.A., Tsao, C.H., 1971. Tympanic organ of Indian meal moth, *Plodia interpunctella* (Hübner), almond moth, *Cadra cautella* (Walker) and tobacco moth, *Ephestia elutella* (Hübner). *International Journal of Insect Morphology and Embryology* 1, 3–10.
- Norris, M.J., 1933. Contributions toward the study of insect fertility—II. Experiment on the factors influencing fertility in *Ephestia kuehniella* Z. (Lepidoptera: Phycitidae). *Proceedings of the Zoological Society of London*, p. 902–904.
- Park, Y.I., Ramaswamy, S.B., Srinivasas, A., 1998. Spermatophore formation and regulation of egg maturation and oviposition in female *Heliothis virescens* by the male. *Journal of Insect Physiology* 44, 903–908.
- Proshold, F.I., 1996. Reproductive capacity of laboratory-reared gypsy moths (Lepidoptera: Lymantriidae): effect of age of female at time of mating. *Journal of Economic Entomology* 89, 337–342.
- Proshold, F.I., Karpenko, C.P., Graham, C.K., 1982. Egg production and oviposition in the tobacco budworm: effect of age at mating. *Annals of the Entomological Society of America* 75, 51–55.
- Ramaswamy, S.B., Shu, S., Park, Y.I., Zeng, F., 1997. Dynamics of juvenile hormone-mediated gonadotropism in the Lepidoptera. *Archives of Insect Biochemistry and Physiology* 35, 539–558.
- SAS Institute, 1990. SAS/STAT User Guide, Version 6. 4th Edition. SAS Institute, Cary, NC.
- Sinha, R.N., Watters, F.L., 1985. *Insect Pests of Flour Mills, Grain Elevators, and Feed Mills and Their Control*. Publication No. 1776E, Research Branch, Agriculture Canada.
- Spurgeon, D.W., Raulston, J.R., Lingren, P.D., Shaver, T.N., 1997. Mexican rice borer (Lepidoptera: Pyralidae) reproductive responses to delayed mating. *Southwestern Entomologist* 22, 195–200.
- Steele, R.W., 1970. Copulation and oviposition behavior of *Ephestia cautella* (Walker) (Lepidoptera: Phycitidae). *Journal of Stored Products Research* 6, 229–245.
- Subramanyam, Bh., Cutkomp, L.K., 1987. Total lipid and free fatty acid composition in male and female larvae of Indian-meal moth and almond moth (Lepidoptera: Pyralidae). *Great Lakes Entomologist* 20, 99–102.
- Svärd, L., McNeil, J.N., 1994. Female benefit, male risk: polyandry in the true armyworm *Pseudaletia unipuncta*. *Behavioral Ecology and Sociobiology* 35, 319–326.
- Unnithan, G.C., Payne, S.O., 1991. Mating, longevity, fecundity, and egg fertility of *Chilo partellus* (Lepidoptera: Pyralidae): effects of delayed or successive matings and their relevance to pheromonal control methods. *Environmental Entomology* 20, 150–155.
- Wakamura, S., 1990. Reproduction of the beet armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae), and influence of delayed mating. *Japanese Journal of Applied Entomology and Zoology* 34, 43–48.
- Walker, P.W., 1991. Effects of delayed mating on the reproduction of *Pectinophora scutigera* (Holdaway) (Lepidoptera: Gelechiidae). *Journal of the Australian Entomological Society* 30, 339–340.
- Ward, K.E., Landolt, P.J., 1995. Influence of multiple matings on fecundity and longevity of female cabbage looper moths (Lepidoptera: Noctuidae). *Annals of the Entomological Society of America* 88, 768–772.
- Wilkund, C., Kaitala, A., Lindfors, V., Abenius, J., 1993. Polyandry and its effect on female reproduction in the green-veined white butterfly (*Pieris napi* L.). *Behavioral Ecology and Sociobiology* 33, 25–33.
- Zar, J.H., 1984. *Biostatistical Analysis*, 2nd Edition. Prentice-Hall, Englewood Cliffs, NJ.