

Effects of Sex Ratio and Pairing Duration on the Biological Performance of Adult Almond Moth, *Ephestia cautella* (Walker) (Lepidoptera: Pyralidae)¹

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ABSTRACT The almond moth, *Ephestia cautella* (Walker) (Lepidoptera: Pyralidae), is a major pest of stored fruit of date palm trees, *Phoenix dactylifera* L. The biological performance of adult almond moths at different sex ratios (female:male) and pairing durations (time that a male and a female were confined together) were investigated under constant conditions. The sex-ratio experiment was performed for six treatments: normal sex ratio (1F:1M), two male-bias sex ratios (1F:2M and 1F:3M), two female-bias sex ratios (2F:1M and 3F:1M), and virgin females alone (1F:0M). The pairing-durations experiment was performed for treatments of 1, 3, 5, 7 days, and the entire lifespan (until either the male or female died). A strong female-bias sex ratio (3F:1M) caused a delay in the maximum number of eggs deposited from the second to the fourth day, reduced the number of laid eggs, and significantly reduced egg hatchability to 77%. A strong male-bias sex ratio (1F:3M) significantly reduced female longevity. A pairing duration over the entire lifespan of the mating pairs significantly reduced male longevity. However, there was no significant effect on number and hatchability of eggs among different pairing duration treatments, which indicates that one day of male confinement with a female is sufficient to have optimum mating and fertilize all the *E. cautella* potential eggs.

KEY WORDS *Ephestia cautella*, Pyralidae, Lepidoptera, sex ratio, pairing duration, reproduction strategies, adult performance

The almond moth, *Ephestia cautella* (Walker) (Lepidoptera: Pyralidae), is a major pest of many stored products, such as fruit of date palm trees, *Phoenix dactylifera* L., cereals, nuts, and dried fruits (Navarro & Gonen 1970, Kamel et al. 1976, Sharma et al. 1978). Almond moths are cosmopolitan pests that favour warm climates (Kamel et al. 1976, Boshra 2007). The economic losses by this pest are due to reductions in quantity and quality of stored products, which leads to difficulties in their marketing (Al Hussain & Jafar 1968).

Population sex ratio is important for predicting mating intensity (Weir et al. 2011). A near equal sex ratio of females and males occurs in most animal species, including insects (Myers 1978, Price 1997, Hardy 2002, Sapir et al. 2008). However, a bias in sex ratio might occur because of many factors (Hardy 1994);

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such as host quality (Price 1997); local mate competition (Werren 1983, Paine et al. 2004); birth, death, migration rates (Sapir et al. 2008); environmental conditions (Wrensch & Ebbert 1993); or infection by microorganisms, such as *Wolbachia* on *Ostrinia furnacalis* (Jiggins et al. 1998, Kageyama et al. 1998, 2003, Hiroki et al. 2002). Although a sex ratio bias may be the result of survival strategy, at other times it may lead to negative effects on natality, decreased fecundity (Price 1997), disrupted population growth (Andersen 1961), limited sperm availability, clutch size alteration, lack of genetic variation, and behavioral constraints (Wrensch & Ebbert 1993).

Insect reproduction also is influenced by the number of times a female mates during her reproductive period (Wang & Shi 2004, McNamara et al. 2008). Both *E. cautella* and a closely related species, *E. kuehniella*, are polyandrous (McNamara et al. 2008, Xu et al. 2008). The initial mating for *E. kuehniella* typically occurs on the first day after emergence and additional mating takes place on the following days (Xu et al. 2008). Each mating period lasts about 120 minutes (Falp et al. 1995, Xu et al. 2008) and mating time depends on the adult nutritional condition and the temperature (Aluja et al. 2009, Katsuki & Miyatake 2009). This study was conducted to investigate the biological performance of *E. cautella* adults at different sex ratios and lengths of time that pairs of males and females were kept together (pairing duration).

Materials and Methods

This study was conducted at the Economic Entomology Research Unit Laboratory, Plant Protection Department, College of Food and Agriculture Sciences, King Saud University, Riyadh, Kingdom of Saudi Arabia. A colony of almond moths was reared on a modified diet composed of a mixture of 1 kg of crushed wheat, hen and broiler poultry feed (each 1.5 kg), and 400 ml of glycerine (Al-azab 2007). Clear-plastic, 1.3-L containers (18, 12, and 6 cm) were used for rearing. The colony and experiments were maintained at 25°C and 65% RH, with a photoperiod of 16:8 L:D inside an incubator (Steridium i500, Queensland, Australia). Only newly emerged adults were used for experiments. To obtain them, pupae were removed from the colony and kept in 60-mL transparent plastic cups (7 cm diam., 2.5 cm tall). Insects were sexed at the pupal stage and adults of each sex were kept in separate containers.

For the sex-ratio experiment, groups of newly emerged adults at different sex ratios were confined until their deaths in a 310-mL plastic jar (7 cm diam., 8 cm tall), positioned upside down. Fiber screen (1 mm²) was used to cover the rim of the jar to let eggs pass down to the 8-cm diameter plastic Petri dishes, which acted as a lid for the jar. Adults were fed by a piece of cotton soaked in sugar solution (10% w/v) that was clipped on the wall of each jar. Air circulation inside the jar was increased by seven small needle holes in the container's walls.

For the first experiment, the effects of sex ratio on adult performance and egg survival were measured. Ten replications of the sex-ratio experiment were performed on six treatments: normal sex ratio (1 Female:1 Male), two male-bias sex ratios (1F:2M and 1F:3M), two female-bias sex ratios (2F:1M and 3F:1M), and virgin females alone (1F:0M). Ratios represented the actual number of adults that were used in the experiment.

For the second experiment, the effects of the time that a male and a female were kept together (pairing duration) had on adult performance were measured. The treatments were individual males and females kept together for durations of 1, 3, 5, 7 days, or for the entire lifespan of the mating pair. Males were separated from females after the designated time durations and kept in individual jars. This experiment was replicated ten times for each treatment.

For both experiments, the number of eggs, their hatching rate, and the incubation period were determined. Also, the reproduction period (pre-oviposition, oviposition, post-oviposition) and total lifespan for both males and females were recorded for each experiment. All data were obtained by daily observations starting from the time females and males were confined in the plastic jar until they died.

All data analysis was conducted using SAS version 9.2 (SAS 2008). Each parameter in the experiment was tested for the normality distribution using PROC UNIVARIATE with the Shapiro-Wilk method. Transformation was applied using square root (x) and $\text{Log}_{10}(x)$ for count data and size data, respectively (Osborne 2010). If the data contained zero (0), we added 1 to the value (Traicevski & Ward 2002). Transformations only were applied for the ANOVA analysis (Wilkinson & Douglas 1998). Repeated measures analysis was used with PROC MIX to evaluate effects of different sex ratio on the eggs deposition trends across days (Table 1). The rest of experiments used PROC GLM for ANOVA to get P -values and protected Least Significant Difference (LSD) tests ($\alpha = 0.05$) for means separation (Madden et al. 1982).

Results

Effects of sex ratio on the performance of adult almond moths. For all sex-ratio treatments, females began depositing eggs one day after their emergence (Table 1). Oviposition continued daily until the end of the female's lives. Repeated measures analysis showed significant differences ($P < 0.0001$) for the three fixed effects sources; the sex ratio effects, the day eggs were laid, and the interaction between sex ratio and day of egg deposition. For most of the sex-ratio treatments (1F:1M, 1F:2M, 1F:3M, and 2F:1M), the maximum eggs deposition was on the second day. However, for the 3F:1M and virgin females, the maximum egg deposition was on the fourth and seventh days, respectively (Table 1). The different sex-ratio treatments did not significantly affect the total number of eggs produced per female. Only virgin females oviposited significantly fewer eggs, and none of them hatched from this treatment (Table 1).

Male longevity was not affected significantly by the difference in sex ratio (Table 2). In contrast, female longevity was affected significantly by the different sex-ratio treatments. In general, a female-bias sex ratio supported a longer female lifespan compared with the male-bias and normal sex-ratio treatments. Females had the shortest lifespan (12.7 days) in the treatment with the strongest male-biased sex ratio (1F:3M). Pre-oviposition, oviposition, and post-oviposition periods of females did not differ significantly for the different sex-ratio treatments (Table 2). Most of the almond moth eggs hatched on the fourth day after oviposition for all treatments (Table 3). However, the percent of hatch at day four for one female-bias sex ratio treatment (3F:1M) was less significantly than other treatments.

Table 1. Total number and hatching success of eggs deposited by almond moth females at six different sex ratios (mean \pm SE).

Sex ratio	Eggs/female at day									Total eggs/female	Percentage of eggs hatched
	1	2	3	4	5	6	7	8	9		
1F:1M	11.0	141.8	83.0	57.5	47.5	44.9	34.1	27.1	13.5	500.7 \pm 44.7 a ^a	86.7 \pm 4.2 a ^a
1F:2M	18.1	96.7	81.7	50.7	57.3	45.9	28.0	23.7	14.2	456.2 \pm 56.7 a	87.7 \pm 2.8 a
1F:3M	4.3	110.6	49.0	47.8	32.8	35.6	27.2	25.5	14.3	501.2 \pm 34.7 a	92.4 \pm 4.8 a
2F:1M	12.4	79.2	51.0	64.1	50.1	47.8	35.4	22.9	22.4	516.1 \pm 67.1 a	83.9 \pm 3.5 ab
3F:1M	15.0	46.3	57.8	75.3	49.5	50.3	35.5	34.1	24.0	451.9 \pm 28.7 a	77.0 \pm 3.0 b
Virgin females	2.1	8.6	7.9	9.4	9.5	9.8	19.3	13.5	9.0	205.2 \pm 38.1 b	0.0 \pm 0.0 c

^aMeans followed by the same letter in the same column are not significantly different (LSD, $\alpha = 0.05$).

Table 2. Longevity of male and female almond moth adults at six different sex ratios (mean \pm SE).

Sex ratio	Total male lifespan			Female lifespan in days ^a		
	in days	Total lifespan	Pre-oviposition period	Pre-oviposition period	Oviposition period	Post-oviposition period
1F:1M	15.3 \pm 2.5 a ^b	14.1 \pm 2.2 bcd ^b	0.6 \pm 0.2 a ^b	0.6 \pm 0.2 a ^b	11.8 \pm 1.8 a ^b	1.8 \pm 0.9 a ^b
1F:2M	15.6 \pm 1.5 a	13.9 \pm 2.5 cd	0.8 \pm 0.2 a	0.8 \pm 0.2 a	11.9 \pm 2.4 a	1.3 \pm 0.6 a
1F:3M	14.7 \pm 1.7 a	12.7 \pm 2.0 d	0.8 \pm 0.2 a	0.8 \pm 0.2 a	9.8 \pm 1.5 a	2.0 \pm 1.0 a
2F:1M	16.9 \pm 2.3 a	18.5 \pm 1.3 abc	-	-	-	-
3F:1M	17.3 \pm 1.8 a	19.6 \pm 1.2 ab	-	-	-	-
Virgin females	-	20.8 \pm 1.9 a	-	-	-	-

^aAt sex ratios of 2F:1M and 3F:1M, data collection for the pre-oviposition period, oviposition period, and post-oviposition period was not possible due to the presence of more than one female.

^bMeans followed by the same letter in the same column are not significantly different (LSD, $\alpha = 0.05$).

Table 3. Percentage of almond moth eggs hatched after 3, 4, and 5 days at five different sex ratios (mean \pm SE) .

Sex ratio	Percentage of eggs hatched at day		
	3	4	5
1F:1M	1.3 \pm 0.6 a ^a	84.1 \pm 5.4 a ^a	3.6 \pm 2.3 a ^a
1F:2M	1.5 \pm 0.6 a	82.1 \pm 3.6 a	4.2 \pm 1.3 a
1F:3M	1.9 \pm 0.6 a	83.8 \pm 4.4 a	6.3 \pm 3.0 a
2F:1M	1.6 \pm 0.5 a	71.0 \pm 5.9 ab	4.5 \pm 1.0 a
3F:1M	1.5 \pm 0.4 a	66.8 \pm 3.7 b	6.6 \pm 1.6 a

^aMeans followed by the same letter in the same column are not significantly different (LSD, $\alpha = 0.05$).

Effects of pairing duration on the performance of adult almond moths. The lengths of time that male and female were confined together (pairing duration) had no significant effect on either the number of almond moth eggs produced or their hatching success (Table 4). This result confirms our observation that almond moth pairs typically mate within a day of being confined, and this initial mating is sufficient to produce the full complement of eggs.

The pairing duration treatments had only a slight effect on male lifespan, and they had no effects on female lifespan (Table 5). If pairs were kept together until one of the adults died (entire lifespan treatment), the male lifespan was reduced significantly (12.6 days) (Table 5). Oviposition and post-oviposition periods of females also were not affected significantly by these treatments.

Discussion

Different sex ratio treatments had little effect on egg-deposition dynamics of *E. cautella*. This finding was similar to what has been reported for other insects in the family Pyralidae, including the olive leaf moth, *Palpita unionalis* (Hübner), which lays its eggs a few days after mating (Kumral et al. 2007) and whose oviposition rate declines with time (Wang & Shi 2004). In our study, the normal

Table 4. Total number of almond moth eggs produced and hatching success for mating pairs held together for different time durations (mean \pm SE).

Pairing duration	Number of eggs	Percentage of eggs hatched
1 day	431.0 \pm 31.7 a ^a	81.0 \pm 3.9 a ^a
3 days	426.1 \pm 40.9 a	74.9 \pm 3.8 a
5 days	386.9 \pm 39.7 a	72.3 \pm 8.5 a
7 days	473.9 \pm 66.7 a	78.5 \pm 4.3 a
Entire lifespan	507.0 \pm 59.0 a	79.7 \pm 3.8 a

^aMeans followed by the same letter in the same column are not significantly different (LSD, $\alpha = 0.05$).

Table 5. Longevity of male and female almond moths held together for different time durations (mean \pm SE).

Pairing duration	Male lifespan in days	Total lifespan	Female lifespan in days		
			Pre-oviposition period	Oviposition period	Post-oviposition period
1 day	14.5 \pm 1.8 ab ^a	10.1 \pm 0.8 a ^a	0.6 \pm 0.2 ab ^a	8.5 \pm 1.1 a ^a	1.0 \pm 0.3 a ^a
3 days	17.2 \pm 1.3 a	12.9 \pm 1.9 a	0.6 \pm 0.2 ab	10.5 \pm 1.7 a	1.8 \pm 0.7 a
5 days	14.1 \pm 2.2 ab	13.9 \pm 2.1 a	1.0 \pm 0.2 a	10.3 \pm 1.9 a	2.6 \pm 0.7 a
7 days	15.4 \pm 1.3 ab	12.7 \pm 1.4 a	0.6 \pm 0.2 ab	10.7 \pm 1.6 a	1.6 \pm 0.6 a
Entire lifespan	12.6 \pm 1.2 b	13.5 \pm 1.3 a	0.4 \pm 0.2 b	11.8 \pm 1.2 a	1.4 \pm 0.7 a

^aMeans followed by the same letter in the same column are not significantly different (LSD, $\alpha = 0.05$).

sex ratio (1F:1M) and male-bias sex-ratio treatments (1F:2M and 1F:3M) exhibited maximum eggs deposition similar to what has been reported for codling moth, *Cydia pomonella* (Vickers 1997). However, for other Pyralidae, such as *Cactoblastis cactorum*, the maximum eggs deposition occurred on the third day (Legaspi et al. 2009). We saw a tendency in the female-bias sex-ratio treatments (3F:1M) and virgin-female treatment for females to retain their eggs longer, perhaps in order to get a sufficient number of males to fertilize their eggs.

Differences in sex-ratios had no effect on the total number of eggs that females laid in our study. However, egg hatchability was significantly reduced in the strongly female-biased sex-ratio treatment (3F:1M). Also, as reported by Barrer (1976), the fecundity of virgin females was reduced and resulted in sterile eggs that did not hatch. On the other hand, male-bias sex ratios tended to increase eggs hatchability, which might be due to sperm competition (Friberg 2006). This result is in contrast to the Hamilton model, which predicts that a strong female bias would be favored (Herre 1998).

The time that pairs of almond moths were kept together did not affect the total number or hatchability of their eggs. We conclude that one day together is sufficient for *E. cautella* to have successful reproduction. This result is in agreement with other studies that report that one mating is sufficient for females to fertilize all of their eggs and to maximize reproductive success (Arnqvist & Nilsson 2000, Mellström & Wiklund 2010). This is because males pass a large number of spermatophores in the first mating, as reported for *Plodia interpunctella* (Ryne et al. 2001).

Interestingly, female longevity was affected by different sex ratios, whereas male longevity was affected by the length of the pairing duration. Female longevity increased when fewer males were present (female-bias treatments), which is similar to the results for the European corn borer (Fadamiro & Baker 1999). Similarly, for codling moth, female longevity increased when mating was delayed (Vickers 1997). Although not consistent, there was a tendency for male longevity to decrease with longer pairing duration. The shortest male lifespan was when they were confined with females for their entire life, which is in consistent with the idea that mating is costly for males (Friberg 2006). Moreover,

it has been reported that if male stalk-eyed flies, *Cyrtodiopsis dalmanni*, had high early mating rates, they would have reduced longevities (Pomiankowski et al. 2005). However, our results did not concur with Taylor et al. (2008) who concluded that females died earlier when exposed continuously to males.

Our knowledge of the effects of sex ratio and pairing duration of *E. cautella* on the day of maximum egg deposition, total numbers of eggs, egg hatchability, and male or female longevities, may help us predict the efficiency of control techniques such as the use of a male attractant (Hodges et al. 1984, Shani & Clearwater 2001). This knowledge also might be used to optimize the mass rearing of this insect for biological control purposes (Fitz-Earle & Barclay 1989, Wrensch & Ebbert 1993).

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