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ORIGINAL ARTICLE

Female delayed mating and shortened pairing duration reduce the reproductive performance of tea mosquito bugs (*Helopeltis bradyi*)

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Abstract

Tea mosquito bugs (TMB; *Helopeltis bradyi*, Hemiptera, Miridae) are a main pest in tea and cacao plantations worldwide. Pheromone-mediated mating disruption (MD) is a promising strategy to manage TMB populations. Experiments were conducted to evaluate the simultaneous effect of TMB female delayed mating (1, 3 and 5 days delayed mating) and pairing duration (1 day, 5 days, and entire lifespan) on several reproductive parameters. Results showed that female delayed mating obviously affected egg number, egg viability, and offspring number, but male delayed mating did not show such effects. Shortened pairing durations had a significant effect on egg viability and offspring number but not on egg number. Increased delayed mating and pairing duration negatively affected adult longevity. In general, we noted that TMB reproductive performance is vulnerable to delayed mating and shortened pairing durations, thus providing essential guidance for the implementation of MD strategies of TMB in the field.

Keywords: delay mating, Helopeltis bradyi, pairing duration, reproduction

Introduction

Indonesia is one of the major producers of tea and cocoa, with 1,951,270 hectares dedicated to cocoa production (Fahmid *et al.* 2018). Efforts to maximize production of both commodities are severely affected by the tea mosquito bug (TMB), which belongs to genus *Helopeltis* (Hemiptera: Miridae) (Saroj *et al.* 2016). With their ability to double their population within 7.52 days, and female bias population in nature (Thube *et al.* 2020), their infestation area and yield loss may reach up to 80% (Mahob *et al.* 2018). Tea mosquito bugs mainly attacks the host plant, where it feeds and lays eggs on young tissues, such as shoots, leaves, and fruit. TMB infestations are usually manifested as a burned appearance or lesions around stylet entry points (Srikumar and Bhat 2013).

Tea mosquito bugs control strategies rely heavily on the use of insecticides (Roy and Gurusubramanian 2009; Saroj *et al.* 2016). However, unexpected failure, contamination, development of insect resistance and environmental problems require the development of alternative control measures within the concept of Integrated Pest Management (IPM) (Stenberg 2017). Promising approaches involve the development of insect olfaction-based control strategies, such as pheromone-based mating disruption (MD) (Benelli *et al.* 2019), the push-pull strategy, and olfaction gene silencing (Malik *et al.* 2016; Soffan *et al.* 2016). These techniques similarly interfere with mate finding and insect reproduction.

Mating disruption strategies have at least two objectives, namely, competition between synthetic and authentic pheromones and misorientation of mating schedules by establishing different pheromone-release points. These techniques aim to interfere with mate-finding events (Benelli *et al.* 2019). Mate-finding interference due to MD causes delayed mating and shortened pairing durations. The characteristics of delayed mating and pairing duration have been investigated in many insect pests, but the available studies often show contradictory effects on reproductive performance (Soffan *et al.* 2012; Yang *et al.* 2017; Wu *et al.* 2018; Zheng *et al.* 2020). Studies on delayed mating and shortened pairing durations in TMB, especially when carried out simultaneously, are scarce. Herein, we report the effects of these two factors on the egg number, egg viability, number of offspring, and adult longevity of TMB. The results may be utilized as a solid reference for evaluating MD strategies for TMB.

Materials and Methods

Tea mosquito bug (TMB) collection and rearing

Tea mosquito bugs at different developmental stages were obtained from a TMB-infested cocoa plantation in Pagilaran, Segayung, Yogyakarta regions of Indonesia, with an average temperature and humidity of 27.8°C and 87%, respectively. Tea mosquito bugs were then raised on cucumber fruit in a rearing room that had the same temperature and humidity as the field. The cucumbers were replaced periodically when they showed early decay symptoms due to TMB feeding. Feeding of TMB on cucumber fruit produces symptoms similar to those found in young tea leaves in the field, that is, circular lesions. Different jars (3 to 4 l volume) were utilized for different rearing stages, including eggs, nymphs, and adults. Adult emergence was observed daily, and the insects were sex-differentiated according to the morphology of the exterior of their abdomen. Adults were individually isolated in plastic cups (500 ml) and fed cucumber fruit until they were utilized in the experiments.

Effects of female delayed mating and shortened pairing duration on reproductive parameters

The principle method for the delayed mating experiment was to separate individual virgin males and females in an individual cage (500 ml plastic cup). They were only paired when females were 1, 3 and 5 days old, and 1-day-old (after emergence) males. Additionally, a male aged 3 days old (after emergence) was paired with a 1-day-old female. The delayed mating experiment was further incorporated with several pairing duration scenarios, where each delayed mating scenario adopted one of three pairing durations of 1 day, 5 days, and an entire lifespan (i.e., until either the male or female died). Once a pairing duration was terminated, both adults were kept in individual cups, similar to the treatment prior to the mating experiment. Adult longevity and female reproductive performance were measured in terms of egg number, egg viability, and number of offspring. These reproductive parameters were evaluated during the pairing period and after insect detachment (i.e., termination of pairing duration). During the experiment, the insects were provided fresh cucumber daily. Used cucumbers were kept individually to observe egg formation and hatchability into offspring.

Statistical analysis

Data analyses were conducted using SAS version 9.2. Five replicates of both male and female were used for all experiments. Factorial analysis (4 × 3 design) was conducted to test interactions between delayed mating and pairing duration. ANOVA was conducted to examine significant differences between treatments. PROC GLM for ANOVA was used to obtain p -values, and protected least significant difference (LSD) tests ($\alpha = 0.05$) were conducted for means separation.

Results

The simultaneous effects of delayed mating and pairing duration on tea mosquito bugs (TMB) were evaluated by conducting factorial analysis as shown in Table 1. Most of the reproductive parameters investigated clearly showed significant interactions with delayed mating and pairing duration, as evidenced by our finding that the majority of the p-values obtained were less than 0.05 (Table 1).

Considering the significant interactions noted between delayed mating and pairing duration in most reproductive parameters studied, cell means comparison further analyzed several TMB reproductive parameters, including egg number, egg viability, and total number of offspring. As shown in Table 2, the highest egg number per female was obtained in the absence of delayed mating of males and females (Table 2, Exp. 1; 234.5). Egg numbers decreased when the female was delayed, as shown in Exps. 1, 2, and 3 (1 day pairing duration; 234.5, 68.4, and 85.8, respectively) and Exps. 5, 6, and 7 (5 days pairing duration; 211.3, 75.6, and 112, respectively). Delays in males did not significantly affect total egg numbers, as shown in Exps. 5 and 8 (5 days pairing duration; 211.3 and 229.3, respectively) and Exps. 9 and 12 (84.5 and 83.4, respectively), with the exception of Exp. 4, which was probably due to the effect of a short pairing duration.

The highest number of viable eggs (Table 2), which was 86.4%, was observed in Exp. 9 (entire lifespan pairing duration; no delayed mating). Decreasing the pairing duration lowered egg viability, as shown in the results of pairing durations of an entire lifespan

Table 1. Factorial analysis of the interactions of delayed mating and pairing duration of tea mosquito bug (TMB) with different parameters

Parameters	*df*	Type III SS	Mean square	*F*-value	*Pr* > *F*
Egg number/female					
Total eggs	6	149,210.5917	24,868.4319	7.08	<0.0001
Paired adult eggs	6	27,694.12304	4615.68717	2.62	0.0311
Detached adult eggs	3	70,453.6033	23,484.5344	10.26	0.0001
Egg viability [%]					
Total eggs	6	4335.35637	722.55939	1.6	0.1737
Paired adult eggs	6	8207.24295	1367.87383	2.48	0.0393
Detached adult eggs	3	3652.17576	1217.39192	2.1	0.1246
Adult age					
Female	6	2691.238725	448.539788	4.52	0.0014
Male	6	9282.384204	1547.064034	24.32	<0.0001

Table 2. Effects of tea mosquito bug (TMB) delayed mating on egg number/female under different pairing durations (mean ± SE) [a, b]

Exp.*	Pairing duration	Delay mating [c]	Total eggs		Total offspring
			no./female	viability [%]	
1	1 day	1 : 1	234.5 ± 19.3 a*	0.6 ± 0.2 de	1.5 ± 0.5 cd
2		3 : 1	68.4 ± 31.2 def	5.9 ± 5.9 e	3.6 ± 3.6 d
3		5 : 1	85.8 ± 14.5 cde	1 ± 1 e	1.2 ± 1.2 d
4		1 : 3	3.3 ± 2 f	2.8 ± 2.8 e	0.3 ± 0.3 d
5	5 days	1 : 1	211.3 ± 32.6 ab	74.8 ± 10.9 ab	151.7 ± 9.3 a*
6		3 : 1	75.6 ± 17.3 cde	48.9 ± 15.6 bcd	40.4 ± 16 bc
7		5 : 1	112 ± 41.5 bcd	36.4 ± 12.2 de	51 ± 23.7 bc
8		1 : 3	229.3 ± 30 a*	78.4 ± 4.7 ab	178.3 ± 23.9 a*
9	Entire lifespan	1 : 1	84.5 ± 47 cde	86.4 ± 8.1 a*	61.8 ± 31.9 b
10		3 : 1	154.5 ± 28 abc	70.6 ± 7.6 abc	104.5 ± 14.6 ab
11		5 : 1	32.3 ± 19.1 ef	36.8 ± 21.6 cde	23.3 ± 13.4 cd
12		1 : 3	83.4 ± 35.2 cde	76.8 ± 10.2 ab	56.8 ± 24.6 b

[a] Means followed by the same letter in the same column are not significantly different (LSD, $\alpha = 0.05$)
[b] The replication number for all experimental units was five replicates
[c] Delay mating female : male (in days)
* Exp. = Experimental unit no.

(Exp. 9; 86.4%), 5 days (Exp. 5; 74.8%), and 1 day (Exp. 1; 0.6%). The older the female (i.e., the greater the delay), the lower the egg viability which was clearly visualized when comparing observations of pairing durations of 5 days, such as in Exp. 5 (female 1 day delayed; 74.8%), Exp. 6 (female 3 days delayed; 48.9%), and Exp. 7 (female 5 days delayed; 36.4%). The same findings were observed in the pairing duration of an entire lifespan, such as in Exps. 9, 10, and 11, which featured females delayed for 1, 3, and 5 days and yielded egg viabilities of 86.4%, 70.6%, and 36.8%, respectively. Egg viability was not affected by male delayed mating, as seen in comparisons of Exps. 5 and 8 (5 days pairing duration), which feature males delayed for 1 (74.8%) and 3 (78.4%) days, respectively, as well as in Exps. 9 and 12 (entire lifespan pairing duration), which featured males delayed for 1 (86.4%) and 3 (76.8%) days, respectively.

The highest total nymph number was observed under a pairing duration of 5 days when males were delayed by 3 days (Exp. 8; 178.3). Assuming that the most important reproductive parameter is nymph (offspring) number, the results of Exp. 8, followed by those of Exp. 5 (no delayed mating; 151.7), are superior to those obtained in the other experiments. These two experiments featured a pairing duration of 5 days. Thus, the optimal pairing duration was 5 days. Under this specific pairing duration, greater female delays significantly reduced the total nymph number, as shown in Exps. 5, 6, and 7, which included females delayed by 1, 3, and 5 days, respectively. Male delayed mating had no negative effect on total nymph numbers, as shown in Exps. 5 and 8, which, respectively, included males delayed for 1 and 3 days (151.7 and 178.3, respectively), and in Exps. 9 and 12, which, respectively, included males delayed for 1 and 3 days (61.8 and 56.8, respectively).

When the insects were paired and detached (Table 3) their reproductive performance was examined. Most of the reproductive parameters were higher in the detached period than in the paired period. For example, in experiments with a pairing duration of 5 days, especially in Exps. 5 and 8, egg number, egg viability, and total number of nymphs were higher in the detached period than in the paired period.

Table 4 shows that longer pairing durations decreased female longevity. This finding was noted in Exps. 1, 4, and 9, which represented pairing durations of 1 day (38.3), 5 days (21.3), and the entire lifespan (16.3), respectively. Reduced female longevity was observed in Exps. 1 and 2 (female 1 and 3 days delayed, respectively), which featured a pairing duration of 1 day. Besides these two experiments, female longevity decreased significantly in all other experiments.

In males (Table 3), the highest longevity was observed in Exp. 4 (66.5), which featured males with a 3-day delay and a pairing duration of 1 day. When we compared males with the same delay under pairing durations of 5 days (Table 4, Exp. 8; 19.5) and an entire lifespan (Exp. 12; 13.8), male longevity significantly decreased. Exps. 9 (25.5) and 12 (13.8) compared males under a pairing duration of an entire lifespan. Here, male longevity was reduced, which means that prolonged pairing durations for males negatively affected their longevity.

Discussion

Mating disruption (MD) has been widely reported to be one of the most effective and environmental-friendly strategies to manage insect pests (Miller and Gut 2015; Wu *et al.* 2018; Benelli *et al.* 2019; Zheng *et al.* 2020). Pheromone-based MD strategies are based on competition between synthetic and authentic pheromones or misorientation of mating schedules (Miller and Gut 2015). Mating disruption strategies interfere with mate finding, thus promoting delayed mating and shortened pairing durations (i.e., the length of time pairs of males and females are kept together) (Soffan *et al.* 2012; Wu *et al.* 2018). Evaluating the effects of both factors simultaneously is necessary to determine the efficiency of MD strategies implemented in the field.

Individual evaluations of either delayed mating or shortened pairing duration alone have been reported in some insects (Yang *et al.* 2017; Wu *et al.* 2018; Zheng *et al.* 2020). This work revealed that both factors have significant interactions, which means they simultaneously affect TMB reproductive strategies. Although some parameters of reproductive performance varied according to a specific mating delay or pairing duration, the effects of both factors showed a generalizable

Table 3. Effects of tea mosquito bug (TMB) delayed mating on egg number/female under different pairing durations during paired and detached periods (mean ± SE)[a, b]

Exp.*	Pairing duration	Delay mating[c]	No. eggs/female		Viability [%]		Total nymphs	
			paired	detached	paired	detached	paired	detached
1	1 day	1 : 1	0.5 ± 0.5 fg	234 ± 19.7 a	0 ± 0 d	0.7 ± 0.2 bc	0 ± 0 f	1.5 ± 0.5 bc
2		3 : 1	1.6 ± 0.7 efg	66.8 ± 31.5 b	0 ± 0 d	5.9 ± 5.9 bc	0 ± 0 f	3.6 ± 3.6 c
3		5 : 1	13.8 ± 4 defg	72 ± 12.2 b	0 ± 0 d	1.1 ± 1.1 c	0 ± 0 f	1.2 ± 1.2 c
4		1 : 3	0.3 ± 0.3 g	3 ± 2.1 c	0 ± 0 d	2.8 ± 2.8 bc	0 ± 0 f	0.3 ± 0.3 c
5	5 days	1 : 1	14 ± 6 cdef	197.3 ± 29.4 a	10 ± 5 cd	79.2 ± 12.4 a	2 ± 1 ef	149.7 ± 8.6 a
6		3 : 1	31.8 ± 9.1 bcd	43.8 ± 18.6 bc	40.9 ± 17 bc	36.2 ± 22.4 bc	17.8 ± 8.1 de	22.6 ± 17.4 bc
7		5 : 1	52.5 ± 9.3 ab	59.5 ± 32.4 b	27.4 ± 9.5 c	45.4 ± 15.2 ab	16 ± 5.7 cde	35 ± 19.2 b
8		1 : 3	35.3 ± 5.5 bcd	194 ± 24.7 a	70.8 ± 21 a	79.2 ± 6.8 a	27.5 ± 10.4 bcd	150.8 ± 17.5 a
9	Entire lifespan	1 : 1	84.5 ± 47 abc	–	86.4 ± 8.1 a	–	61.8 ± 31.9 abc	–
10		3 : 1	154.5 ± 28 a	–	70.6 ± 7.6 ab	–	104.5 ± 14.6 a	–
11		5 : 1	32.3 ± 19.1 cde	–	36.8 ± 21.6 bc	–	23.3 ± 13.4 cde	–
12		1 : 3	83.4 ± 35.2 ab	–	76.8 ± 10.2 a	–	56.8 ± 24.6 ab	–

[a] Means followed by the same letter in the same column are not significantly different (LSD, $\alpha = 0.05$)
[b] The replication number for all experimental units was five replicates
[c] Delay mating female : male (in days)
* Exp. = Experimental unit no.

Table 4. Effects of tea mosquito bug (TMB) delayed mating on adult age under different pairing durations (mean ± SE) [a, b]

Exp.*	Pairing duration	Delay mating [c]	Ages	
			female	male
1	1 day	1 : 1	38.3 ± 6.3 a*	36.5 ± 7.8 bc
2		3 : 1	41.8 ± 8.5 a*	11.2 ± 1 ef
3		5 : 1	18.8 ± 4.3 bcd	7 ± 0.7 gh
4		1 : 3	9.8 ± 7.8 d	66.5 ± 1.5 a*
5	5 days	1 : 1	21.3 ± 3.8 abc	60 ± 2.9 ab
6		3 : 1	11 ± 0.5 d	46.6 ± 1.1 b
7		5 : 1	12.3 ± 0.3 cd	9.5 ± 1.8 gf
8		1 : 3	23.8 ± 3.7 ab	19.5 ± 1.8 cd
9	Entire lifespan	1 : 1	16.3 ± 4.8 bcd	25.5 ± 11.1 de
10		3 : 1	20.3 ± 1.8 abc	13.3 ± 1.5 def
11		5 : 1	17.5 ± 4.5 bcd	4.3 ± 0.6 h
12		1 : 3	13 ± 1.8 cd	13.8 ± 1.3 de

[a] Means followed by the same letter in the same column are not significantly different (LSD, $\alpha = 0.05$).
[b] The replication number for all experimental units was five replicates
[c] Delay mating female : male (in days)
* Exp. = Experimental unit no.

pattern. Female delayed mating, but not male delayed mating, obviously affected egg number, egg viability, and offspring number. This result is in line with previous findings that delayed mating has a negative effect on reproductive performance, which means adult insects are more vulnerable to alterations in reproductive strategies than younger insects (Wu *et al.* 2018; Lai *et al.* 2020; Zheng *et al.* 2020). However, some reports have indicated that delayed mating leads to better reproductive success and could be considered advantageous in some species, such as in *Planococcus ficus* (Lentini *et al.* 2018), or *Cimex lectularius* (Wang *et al.* 2016). We found that female delayed mating had stronger effects on the reproductive parameters investigated than male delayed mating. Many previous studies have indicated that delayed mating in both sexes equally affects reproductive success, such as in *Phauda flammans* (Zheng *et al.* 2020), *Cnaphalocrocis medinalis* (Kawazu *et al.* 2014), *Chilo partellus* (Dhillon *et al.* 2019), *Ectropis obliqua* (Yang *et al.* 2017), and *Plutella xylostella* (Wang *et al.* 2011). Interestingly, when we evaluated TMB reproductive parameters in the detached and paired periods, detached periods clearly showed higher reproductive success than paired periods. We speculate that this finding may be attributed to the availability of space, which allows females to focus on reproductive activities without the presence of males. In this case, males may negatively affect female reproductive success.

This study confirmed that decreasing or shortening pairing durations had a negative effect on egg viability and offspring number but not on egg number. These findings may be related to the presence of sperm deposited by males, which regulates fertility and egg viability. Egg viability also seemed to be affected by female delayed mating; specifically, the older the female (i.e., the greater the delay), the lower the egg viability. This result is interesting because some insects, such as *Ephestia cautella*, are not affected by different pairing durations (Soffan *et al.* 2012).

These findings reveal that TMB is vulnerable to strategies causing the shortening of pairing duration, even if mating events occur within a short time. Frequent mating has been reported to affect fitness and vulnerability to predation (Rowe 1994) and physical conditions (von Helversen and von Helversen 1991).

Increases in delayed mating and prolonged pairing durations have negative effects on male and female lifespans. Reduced female longevity was also correlated with increased reproductive performance. This result is in line with earlier reports demonstrating that adult age determines mating success because of the correlation of this parameter with insect reproductive maturity during fertilization (Bonduriansky and Brassil 2002). Other scholars found that adult longevity does not always correlate with delayed mating, as observed in *Phauda flammans* (Zheng *et al.* 2020). Delayed mating in tobacco cutworm, *Spodoptera litura*, increased the longevity of the insects (Wu *et al.* 2018). We further noted an obvious age reduction of fresh males when they were paired with older females (female 5 days delayed; Exp. 3, 7.0; Exp.11, 4.3). Older females appeared to exert negative effects on fresh males when they were paired, possibly because fresh males would not choose older females in the field.

Given these reports, we noted that TMB reproductive performance was sensitive to environmental changes that induced the occurrence of delayed mating and shortened pairing duration. This finding may lead to potential implementations of MD strategies to control TMB infestations in tea or cocoa plantations.

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