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RESEARCH

Analysis of the Mating and Reproductive Traits of *Plutella xylostella* (Lepidoptera: Plutellidae)

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ABSTRACT. The reproductive traits of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) were investigated and analyzed by different analytical methods. Simple statistical analysis showed relatively higher mating rates maintained from 21:00 to 2:00, thereafter dropping to a minimum at about 18:00. Mating rates were affected by female and male age. Mating was most likely to take place between females and males that were 1 d old. Correlation and factor analysis indicated that mating delayed females have a relatively lower and unsuccessful mating rate and relatively shorter copulation duration, with lower egg hatchability and fecundity; in addition, the mating delayed male would reduce female's fertility. Delay of mating prolonged life of both males and females. A higher and successful mating rate would cause a higher egg hatchability and fecundity. Canonical correlation analysis showed that mating age and successful copulation of female play a decisive role for her fecundity and longevity, and mating age and mating rates of male play a decisive role for his longevity.

Key Words: fecundity, longevity, mating delay, multifactorial analysis, mating rate

Diamondback moth *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) is one of the most serious pests of cruciferous crops throughout the world, particularly in tropical and subtropical countries (CABI Compendium 2004). Crop damage is caused by its larval feeding and excretion (Vanichpakorn et al. 2010). This pest is hard to control due to its high reproductive rate and the level of resistance it has developed to various insecticides (Shelton et al.1993, Mohan and Gujar 2003, Sayyed and Wright 2005, Zhao et al. 2006). Simultaneously, there is increased interest in ecofriendly methods to control diamondback moth, such as mating disruption, which can only be successful following studies of reproductive behavior and chemical ecology of diamondback moth (Schroeder et al. 2000, Maxwell et al. 2006, Guo and Qin 2010).

During a mating disruption program, many females should miss their optimum age of mating, resulting in decreased fecundity (Huang and Subramanyam 2003, Fitzpatrick 2006, Jones et al. 2008). Wang et al. (2011) investigated the effects of delayed mating on the fecundity, longevity, and fertility of diamondback moth females. Besides mating age, many mating traits including mating rate, time of mating, copulative rate, copulative duration, etc. had some relationship with diamondback moth reproduction (Uematsu et al. 1989, Pivnick et al. 1990, Talekar and Shelton 1993). Disruption of any of these traits will affect the total reproductive output of diamondback moth. However, little data exist about all of these mating traits of diamondback moth on their reproduction. This is caused by the need for a systematic experimental set-up and practical statistical analysis methods.

There are complex relations among mating and reproductive variables. Many times, it is difficult to find a regular pattern among these variables by a simple analysis. Multiple statistical examines the relationships among multiple variables. Among the methods of multiple statistical analyses, principal components analysis (PCA), and factor analysis are frequently used in the researches of animal ecology and behavior. They aim to reduce numerous measures to a small set of the most important summary scores (Tabachnick and Fidell 1996, Budaev 2010). Researchers often try to interpret principal components and significant clusters to obtain a better understanding of the patterns of correlations between the original variables. Canonical correlation analysis is also a multivariate statistical model that facilitates the study of interrelationships among sets of multiple dependent variables and multiple independent variables (Green and Carroll 1978).

Up to now, some correlations between the traits of diamondback moth are not clear, e.g., Tan et al. (2011) indicated a positive correlation between the moth age and copulation duration, but Wang et al. (2011) did not show a significant correlation between them. In practice, a better understanding of the traits and their correlations are useful to guide the biocontrol of diamondback moth. For example, diamondback moth reproduction was reduced by disturbing its mating behaviors through interference with sex pheromone transmission; in the future, the insect pest can be controlled by breaking the links among the traits that determine reproductive success. In this study, 11 mating and reproductive traits of diamondback moth were investigated and analyzed by several analytical methods. Our hypothesis is that the reproduction of diamondback moth is under the control of a set of mating and reproductive traits. Elucidation of the mating and reproductive traits of diamondback moth will provide some insight into potential pest biocontrol methods.

Materials and Methods

Insect Rearing. Larvae of diamondback moth, *P. xylostella* (L.) (Lepidoptera: Plutellidae) were collected from cabbage plants (*Brassica oleracea*) (L.) in Beijing (39.5° N, 116.2° E), China, from July to August 2011, and reared in an insectarium under the conditions of 26 ± 2°C, 14:10 (L:D) h photoperiod, and 60–70% relative humidity (RH), until pupation. Two-wk-old radish plants (*Raphanus sativus*) (L.) with two fully expanded true leaves were used as larval food. After eclosion, the moths were fed continuously with 10% sucrose solution. Male and female were segregated by their form and structure at their pupal stage, and then all virgin moths used in the bioassays were kept under the same environmental conditions as that described earlier. An adult was considered 1-d old on the day of its eclosion.

Data Collection. Pupae were placed singly into glass tubes (5 cm tall by 3 cm in internal diameter) with moist cotton in the bottom and covered with a small mass of cotton. The date of each adult emergence was recorded on the tube. All moths were sorted into groups based

Table 1. Data of reproductive traits of diamondback moth, *P. xylostella* (L.)

Mating age of females (days) X1	Mating age of males (days) X2	Mating rates (%) X3	Mating times X4	Successful copulation rate (%) X5	Copulative duration (min) X6	Female fertility (%) X7	Egg hatchability (%) X8	Fecundity (egg) X9	Longevity of females (days) X10	Longevity of males (days) X11
1	1	100	2.75 ± 0.44	84.17 ± 5.10	59.09 ± 3.22	85.00	88.93 ± 1.71	95.06 ± 5.07	5.50 ± 0.14	5.00 ± 0.13
2	2	100	2.33 ± 0.76	89.36 ± 6.18	53.18 ± 4.23	90.00	80.71 ± 8.02	79.13 ± 12.67	5.70 ± 0.21	5.10 ± 0.10
3	3	90	2.11 ± 0.39	70.37 ± 15.16	41.58 ± 5.53	70.00	67.69 ± 4.33	71.57 ± 12.00	7.40 ± 0.27	6.20 ± 0.13
4	4	55	1.83 ± 0.37	73.05 ± 10.40	44.09 ± 5.87	72.22	57.20 ± 5.62	63.67 ± 7.11	7.72 ± 0.11	6.39 ± 0.12
5	5	80	1.79 ± 0.31	75.00 ± 12.50	53.33 ± 5.27	70.00	63.35 ± 6.27	43.93 ± 5.75	8.70 ± 0.19	7.50 ± 0.15
6	6	50	1.50 ± 0.34	85.71 ± 8.17	49.00 ± 5.93	47.37	37.63 ± 8.87	43.09 ± 7.97	9.74 ± 0.27	9.05 ± 0.21
3	1	81	2.07 ± 0.30	92.92 ± 5.24	60.00 ± 3.92	80.00	74.11 ± 4.80	70.56 ± 13.39	7.45 ± 0.25	5.73 ± 0.30
4	1	60	2.58 ± 0.38	68.75 ± 13.15	50.00 ± 6.83	90.00	67.95 ± 10.01	56.67 ± 15.56	7.33 ± 0.37	5.56 ± 0.24
5	1	54	2.28 ± 0.42	68.21 ± 10.76	53.21 ± 5.73	78.95	56.48 ± 7.63	56.50 ± 8.12	8.90 ± 0.18	5.40 ± 0.27
6	1	50	2.88 ± 0.85	64.81 ± 12.56	40.50 ± 6.22	88.89	43.56 ± 10.52	56.38 ± 12.96	9.89 ± 0.31	6.22 ± 0.28
1	3	95	2.07 ± 0.30	83.34 ± 7.76	58.28 ± 5.30	73.68	77.66 ± 3.57	82.00 ± 5.79	6.13 ± 0.26	5.67 ± 0.16
1	4	95	2.58 ± 0.38	89.42 ± 4.81	59.39 ± 3.20	72.22	70.18 ± 4.31	83.32 ± 6.19	6.30 ± 0.15	6.70 ± 0.15
1	5	90	2.28 ± 0.42	82.55 ± 6.35	52.65 ± 3.31	76.47	76.76 ± 3.49	72.65 ± 10.61	6.11 ± 0.15	7.63 ± 0.16
1	6	70	2.88 ± 0.85	92.50 ± 5.26	69.13 ± 6.97	62.50	80.17 ± 6.80	70.88 ± 10.96	6.11 ± 0.20	8.11 ± 0.20

There were totally 14 age combinations of female and male, each age combination contained a number 40 of female and male ($N = 40$). The number after " ± " is standard errors. "VAR" variables: X1–X6; "WITH" variables: X7–X11.

on age in days from 1 to 6 d old. Overall, there were 14 age combinations of female and male ages. Each age combination contained an equal number ($N = 40$) of female and male individuals (Table 1).

Moth traits were divided into 11 variables according to the characters of mating and reproduction of *P. xylostella* (Table 1). For the canonical correlation analysis, two groups of 11 variables were separated as follows: X1–X6 as independent variables, and X7–X11 as dependent variables. These 11 variables were defined as follows:

X1: Mating age of female (days): the days a female adult from emergence to its mating. X2: Mating age of male (days): the days a male adult from emergence to its mating. X3: Mating rate (%) = (Copulative adults/Total adults) × 100%. X4: Mating times: the number of mating of a male or a female throughout their lives. X5: Successful copulative rate (%) = (Reproduced copulations/Total copulations) × 100%. X6: Copulative duration (min): the time length for a copulation. X7: Female fertility (%) = (Egg-laying female adults/Mated female adults) × 100%. X8: Egg hatchability (%) = (Hatched eggs/Total eggs) × 100%. X9: Fecundity (eggs): the total eggs produced by one female adult. X10: Longevity of female (days): the days a female adult from emergence to its death. X11: Longevity of male (days): the days a male adult from emergence to its death.

Observations were conducted for 24 h after treatments were established. All the copulative behaviors were observed and counted every 10 min during this period. Observations were conducted under a red light during the scotophase.

In addition to the observations earlier, a choice experiment was conducted with individuals of varying ages of female and male to compare the copulation rates of different combinations. Six females of different ages (from 1- to 6-d old) were marked with different color paints (a pre-experiment of ours proved the paints had no effect on the courtship and mating of diamondback moth), were put into a big beaker ($\Phi = 10$ cm), then one male (1-, 2-, or 3-d old) was put into the beaker, which was covered with a piece of gauze. Copulation was observed under red light at room temperature from 20:00 to 21:00. In total, nine combinations of the choice experiment were examined: one male of 1 d old with six females of the 6 ages (3 repeats), one male of 2 d old with six females of the 6 ages (3 repeats), and one male of 3-d old with six females of the 6 ages (3 repeats).

Data Analysis. Correlations between the 11 variables were tested first. Following this, PCA was conducted to create uncorrelated principal components from the original variables. Factor analysis was used to find the variables which were most useful for discriminating between 11 variables of reproduction. Finally, for giving a synthetical correlation analysis, canonical correlation coefficients were calculated from the two data sets. These 11 variables were divided into two groups. The first one was an independent group related to mating traits (X1–X6) and the second one was dependent group related to reproduction traits (X7–X11).Factor scores estimated the actual values of individual observations on the factors, and factor loading based on the correlation between variables and factors.

All of the statistical analysis was performed by using SAS 9.0 statistical software.

Results

Mating Rate. Curves undulated differently from the mating rates of the 14 age combinations of female and male (Fig. 1). Mating rates were higher from 21:00 to 7:00, and lower from 7:00 to 19:00. The mating rates were affected by age of female and male. Mating was most likely to take place between females and males that were 1-d old. It can be seen in Figure 1 that some of the age-delayed couples could mate during day time, especially the female age-delayed couples. Results from the choice experiment showed that males of different ages unanimously select 1-d-old females to copulate.

Correlation Matrix.

Negative Correlations. The correlation coefficients (Table 2) showed negative relationships between female mating age (X1) and mating rate (X3), egg hatchability (X8), fecundity (X9), successful copulation rate (X5), and copulative duration (X6), all of which were statistically significant. These indicate that that older females mated less, fertilized fewer eggs, and had lower fecundity, less successful copulation and shorter copulative duration. For males, significant negative correlations were observed between mating age (X2) and female fertility (X7). This indicates that older males were less successful in fertilizing females. Other negative correlations appeared, respectively, between mating rate (X3) and female longevity (X10); female fertility (X7) and male longevity (X11); egg hatchability (X8), fecundity (X9), and female longevity (X10). All of these relationships indicate that older females and males showed less mating, were less fertile, and showed less fecundity.

Positive Correlations. Significant positive correlations were observed between female mating age (X1) and her longevity (X10), male mating age (X2), and his longevity (X11). These suggest that a mating delayed female or male would live longer. The additional positive correlations appeared respectively between mating rate (X3), egg hatchability (X8), and fecundity (X9); successful copulation rate (X5) and copulative duration (X6); egg hatchability (X8) and fecundity (X9). All of these indicate that the higher the mating rate and successful copulation rate the higher of the egg hatchability and copulative duration, and the fecundity and hatchability are positively correlated.

Factor Analysis and Clustering. PCA of the reproductive trait analysis extracted two factors with eigenvalues of more than one. Cumulatively, these factors explained 79.68% of the total variability in the data. The first factor (F1) explained 51.16% of the total variability, whereas the second factor (F2) explained 28.52% of the total variability. A classification was done by FA (Kaiser-Meyer-Olkin = 0.552, Bartlett Approx. Chi-Square = 155.128, df = 55, Significance = 0.000) that sorted out four significant clusters from 11 variables, in which, X1–X10 characterized female mating age and her longevity; X2–X11 characterized male mating age and his longevity; X4–X7 characterized mating times and female fertility, and X3, X5, X6, X8, and X9 characterized the multimating property and fecundity (Fig. 2). Each of these clusters from a specific or a synthetical angle showed the closer relationships between the relevant variables.

Canonical Correlation. Tests of dimensionality for the canonical correlation analysis indicated that two of the five canonical dimensions are statistically significant at the 0.05 level. The first canonical correlation coefficient had a canonical correlation of 70%, and second was 26%. The absolute correlation information from the two canonical correlation coefficients was over 96% of the total.

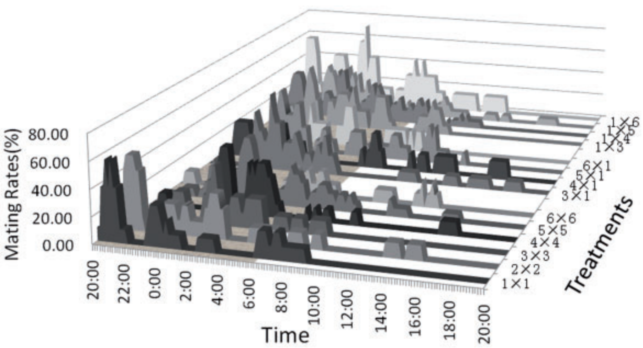

Fig. 1. Rhythms of mating in *P. xylostella*. Observations were conducted every 10 min. for 24 h. In number 1 × 2, number 1 is the female age (days), and number 2 is the male age (days). The scotophase is from 20:00 to 6:00, and the photophase from 6:00 to 20:00.

Table 3 presents the standardized canonical coefficients for the first two dimensions across both sets of variables. The first canonical dimension I1 from independent variables showed two bigger coefficients from X1 and X5, and D1 from dependent variables showed two bigger coefficients from X9 and X10. These showed a closer correlation between female mating age and successful copulation rate of independent variables, and fecundity and longevity of female with dependent variables. The second canonical dimension I2 from independent variables showed two bigger coefficients from X2 and X3, and D2 from dependent variables showed two bigger coefficients from X10 and X11, these meant their closer correlation came from mating age of male and mating rates of independent variables, and longevity of female and male from dependent variables. The biological meaning of the canonical correlation analysis should be that the mating age and successful copulation of female play a major role for her fecundity and longevity, and the mating age and mating rates of male play a major role for his longevity.

Discussion

The results from this study showed that relatively higher mating rates were observed from 21:00 to 2:00, decreasing after this until about 18:00. This contrasts with a study showed three mating peaks during a day, namely 12:30, 0:30, and 6:30 (Tan et al. 2011). By a comparison, it found some difference of the insect rearing conditions between them and ours (Tan et al.: 25 ± 0.5°C, 12:12 (L:D) h photoperiod, and 80% RH; this study: 26 ± 2°C, 14:10 (L:D) h photoperiod, and 60–70% RH). The discrepancies of these results maybe mainly come from the difference between light and dark conditions. And considered with the present results, it is possible that diamondback moth can mate at different times within a day and night. During day time, a relatively higher mating rate appeared when 1-d-old male mates with a female over that age (mating delayed female); conversely, relatively lower mating rates were observed when 1-d-old female mates with a male over that age.

By raising its copulative frequencies, female may make up for the loss of deterioration in viability of ova with time (Wenninger and Averill 2006). Male age does not appear to be a major factor determining mating success in diamondback moth, as long as the female is young. From this study, mating is most likely to take place between 1-d-old females and males during night time. That is consistent with the results from Pivnick et al. (1990) and Ohira (1979) which showed that the mating occurs during the first 4–15 h following emergence with a peak between 1 and 2 h of scotophase.

Any delay in mating age will affect reproduction. In this study older females had lower mating rate, successful copulation, copulative duration, egg hatchability, and fecundity; and the mating delayed male would reduce the female fertilization. In this study, the females laid their eggs in the presence of their male partner. The results could not

Table 2. Correlation matrix between 11 variables of diamondback moth, *P. xylostella* (L.)

	Mating age of females (days) X1	Mating age of males (days) X2	Mating rates (%) X3	Mating times X4	Successful copulation rate (%) X5	Copulative duration (min) X6	Female fertility (%) X7	Egg hatchability (%) X8	Fecundity (egg) X9	Longevity of females (days) X10	Longevity of males (days) X11
X1	1										
X2	−0.104	1									
X3	−0.806**	−0.034	1								
X4	−0.382	−0.382	0.137	1							
X5	−0.626*	0.347	0.519	−0.007	1						
X6	−0.643*	0.191	0.407	0.288	0.768**	1					
X7	−0.124	−0.830**	0.217	0.554*	−0.290	−0.130	1				
X8	−0.893**	−0.134	0.820**	0.395	0.516	0.642*	0.357	1			
X9	−0.882**	−0.250	0.783**	0.466	0.474	0.434	0.346	0.807**	1		
X10	0.961**	−0.000	−0.808**	−0.367	−0.575*	−0.582*	−0.257	−0.939**	−0.869**	1	
X11	0.189	0.897**	−0.316	−0.338	0.221	0.068	−0.834**	−0.409	−0.500	0.318	1

*r**∼significant at the level α = 0.05, and *r*** ∼ extremely significant at the level α = 0.01; df = 12.

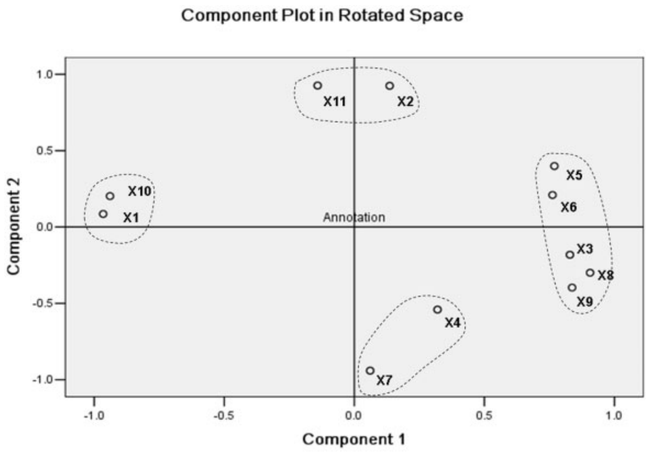

Fig. 2. Cluster of the reproductive traits by factor analysis. Extraction method: Principal Component Analysis. Rotation method: Varimax with Kaiser Normalization. Rotation converged in 3 iterations.

Table 3. Standardized canonical coefficients for the independent (I) and dependent (D) variables

$I1 = -0.8967x1 + 0.1527x2 - 0.0006x3 + 0.1667x4 + 0.2743x5 - 0.2658x6$

$D1 = 0.1295x7 - 0.0373x8 + 0.5819x9 - 0.5961x10 + 0.5266x11$

$I2 = -0.1068x1 - 0.9076x2 + 0.2553x3 - 0.0154x4 - 0.2157x5 + 0.0947x6$

$D2 = 0.2733x7 + 0.4719x8 + 0.3506x9 + 0.7767x10 - 0.6223x11$

tell that without the presence of the male if females were left to lay their eggs, and whether a single copulation was enough to have a decent brood.

This study indicated a negative correlation between the moth age and copulation duration, which are different to the studies of Wang et al. (2011) and Tan et al. (2011). The former did not show a significant correlation between them but the latter indicated a positive correlation. A positive correlation between copulation duration and male mating times was reported by Wang et al. (2005), but this correlation was not existent from this study. Partial reason of these differences maybe come from the insect-rearing conditions among the studies (Tan et al.: 25 ± 0.5°C, 12:12 (L:D) h photoperiod, and 80% RH; Wang et al.: 25 ± 1.0°C, 16:8 (L:D) h photoperiod, and 75% RH; this study: 26 ± 2°C, 14:10 (L:D) h photoperiod, and 60–70% RH). All of these aspects need additional researches.

Some researchers explained that females by extending mating time can get a little more sperm and nutrients transferred from male semen (Hirai and Kimura 1999). Males by extending mating times not only transfer more sperm and nutrition to females, but also as a way to defend against other males and avoid sperm competition (Alcock 1995, Simmons 2001). Mating delay phenomenon is similar as those seen in other insects (Unnithan and Paye 1991, Vickers 1997, Fadamiro and Baker 1999, Fraser and Trimble 2001, Torres-vila et al. 2002, Stelinski and Gut 2009). It may be attributed to the energy conservation. If the moths cannot be mated quickly after their emergence, both males and females have to spend part of their energy surviving in order to have a chance to mate. The longer they wait for mating the less of their energy preserved, as soon as they are mated, the energy for further copulation is less than before, fertility and fecundity are decreased afterwards. This implies that energy consumption for reproduction is critical and correlated to the energy resources (food availability). The results of this study emphasize that 1-d-old females are at peak reproductive capacity, any delay in mating beyond this age may result in reduced reproduction. In practice, these results are useful for understand the control method of mating disruption of diamondback moth, in which a lot of males can be trapped and killed, such that female moths cannot find a male to mate with immediately so that their longevity will be prolonged and their fecundity will be decreased.

In this study, besides the close correlations between diamondback moth mating age and reproduction traits, many significant correlations arose from a specific or a synthesis angle of the multiple statistical analysis. From the simple correlations, the closer relationships arose between the relevant variables, such as mating rate and female longevity, egg hatchability and fecundity, successful copulation rate and copulative duration etc. From a specific or a synthetical angle factor analysis and canonical correlation analysis showed the closer relationships between the relevant variables.

In summary, any disadvantageous effect on diamondback moth mating will cause a reproduction defect. We think, these results should be helpful for the plant protection workers to work out new diamondback moth controlling plans.

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Conflict of Interest

There is no conflict of interest between authors.

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