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ORIGINAL ARTICLE

Daily rhythmicity in the sexual behaviour of *Monema flavescens* (Lepidoptera: Limacodidae)

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Abstract. Daily rhythmicity in the sexual behaviour of *Monema flavescens* Walker (Lepidoptera: Limacodidae) was studied under laboratory conditions. There was a distinct diel periodicity in female calling, male responsiveness and mating behaviour of *M. flavescens*. As females aged there was an advance in the onset and more time spent calling. One day old females started calling 4 h after the onset of the scotophase, and 5 to 6 day old females called during the first hour of the scotophase. About 34.5% of females called on the night they emerged (1 day old) and the peak in calling of 97.8% was recorded for 2 day old females, after which the incidence of calling decreased rapidly with advancing age. Wind tunnel and copulation tests showed that males were sexually mature on the third night and female moths on the second night. The highest value for the percentage mating was recorded for 3 day old virgin females 4 to 6 h after the onset of the scotophase. In field tests, traps baited with 2 day and 3 day old virgin females captured more males than any other trap and most males were captured 4 to 6 h (1 to 2 day old), 3 to 5 h (3 to 4 day old) and 2 to 4 h (5 to 6 day old) after the onset of the scotophase. These results indicate that there is a daily rhythm in the reproductive behaviour of *M. flavescens* and provides a better understanding of its sexual behaviour.

INTRODUCTION

The Nettle caterpillar, *Monema flavescens* Walker, 1855 (Lepidoptera: Limacodidae), is a serious defoliator of a wide variety of trees (Carrillo et al., 2012; Wang et al., 2013; Yang et al., 2016a) in many areas in eastern Asia including Japan, China, Korea and Russia (Siberia) etc. (Lammers, 2004; Yang et al., 2016b). Currently, *M. flavescens* is increasing in abundance in China and overwintering cocoons are easily found in orchards and parks (Ju et al., 2008; Li et al., 2010, 2013; Han et al., 2013). Currently, the control of this insect pest relies mainly on spraying with chemical insecticides. However, as apples, pears and other fruit mature when the larvae of this pest are most active using pesticides to control them poses serious problems. Use of the female-produced sex pheromone may offer a promising alternative tool for controlling this pest. As recorded for other pests (Blackmer et al., 2008; Jing et al., 2010; Yang et al., 2012; Youm et al., 2012; Naka et al., 2018), sex pheromones could provide an environmentally friendly and effective technique for controlling these pests by selectively capturing the males and so reducing the likelihood of females finding a mate.

In this study, daily rhythmicity and the effects of age on both calling behaviour were investigated in *M. flavescens*. These studies could be helpful in improving our understanding of chemical communication in the reproductive behaviour of Chinese populations of *M. flavescens* and of how to use pheromones to detect, monitor and mass-capture this pest in the field.

MATERIALS AND METHODS

Insects

Cocoons were collected from pear and apple trees in Luanxian County, Hebei Province, in late April 2014 and 2015. The cocoons were kept at 25 ± 2°C, 75 ± 5% relative humidity (RH) and under a natural photoperiod until adult emergence. The adults of *M. flavescens* started to emerge at the end of May. After emergence, the male and female moths were immediately segregated into different cages (40 × 40 × 60 cm; 15 moths per cage) containing 10% (wt/vol) sugar solution in different rooms. One room was used for observing calling and copulation and the other for wind tunnel experiments under a 14L : 10D natural photoperiod (sunrise about at 5:00 and sunset at 19:00). A single red incandescent light bulb providing a light intensity of approximately 0.5 lux was used to observe sexual behaviour in both rooms. In-

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dividuals were considered to be 1 day old (1 d) between 0 and 24 h after emergence.

Calling behaviour

Observations of 30 *M. flavescens* females were made every 15 min throughout the 10 h of the scotophase because preliminary observations indicated that adults were not sexually active during the photophase. Calling behaviour of female moths was accompanied by the full exposure of their ovipositors. If a female called during two consecutive observations, it was considered to have been calling for 30 min. If a female was recorded calling on only one of the two observations, it was considered to have been calling for 15 min. Calling behaviour was recorded on three occasions (three replicates) for a total of 90 females.

Wind tunnel tests

The wind tunnel experiments were performed in a glass wind tunnel (195 × 60 × 60 cm) maintained at 22 ± 2°C and 75% ± 3% RH, with an air speed of 0.5 m/s and a light intensity of approximately 0.5 lux. Extract of the pheromone glands of five females was reduced to 10 µL under a gentle stream of N_2 and then dispensed onto a 2.0 cm^2 filter paper placed in the wind tunnel. The response of *M. flavescens* males was tested daily using moths aged from 1 to 6 days old, at different times during the scotophase and when they were most sexually active (3 day old). The males were acclimated for at least 1 h to the light intensity and airflow in the tunnel before they were exposed to the pheromone. The males were released 150 cm downwind from the pheromone source. Two minutes were allotted for the male to respond and when there was no response the male was replaced. Once flight was initiated, the males were observed until they stopped responding. All treatments were tested in random order with three replicates, with each replicate consisting of approximately 15 males. The responses of the males was recorded in terms of the following behaviour: takeoff, directed flight, landing on the source and attempts at copulation.

Copulation

In order to record mating activity, six groups of 20 pairs of 1 to 6 day old virgin males and females were placed individually in small cages (60 × 60 × 60 cm) and mating recorded every 15 min during the test period. All these experiments were done in a test room at 25 ± 1°C, 75 ± 1% R.H and under a 14L : 10D photoperiod. Mating pairs were gently transferred into a small cage (30 × 30 × 30 cm) for measuring copulation duration. Mating pairs and the other moths were not disturbed during this process. When the scotophase ended at 5 a.m., females were dissected, and copulation was determined by the presence of a spermatophore. The percentages of pairs starting to copulate at different times during the scotophase were calculated for all the groups. Three replicate groups were observed, with a total of 60 pairs in each group.

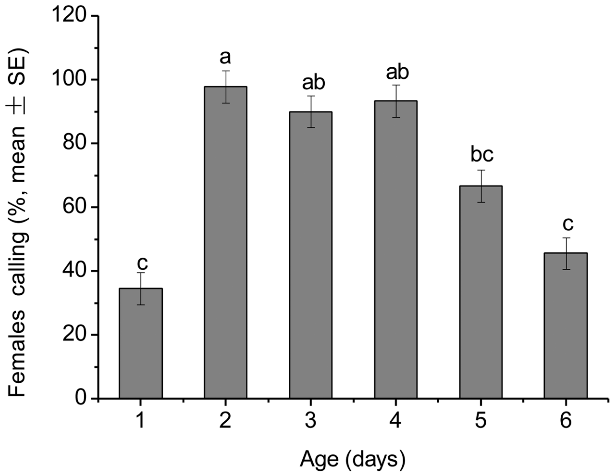

Fig. 1. The percentage of females of *Monema flavescens* of different ages calling during the scotophase. Percentages are means (± SE). The different letters indicate significant differences at P ≤ 0.05 according to Tukey's HSD of arcsine-transformed data.

Field tests

Field tests were conducted in pear trees in Luanxian County, Hebei Province (39°66´N, 118°72´E), in June 2014. White delta sticky traps were suspended at a height of 1.5 m at intervals of 50 m. Virgin females aged 1 to 6 days old were placed in cages as bait beneath the roof of the traps. To compare the attractiveness of the virgin females, control traps without females were also used. The trap catches were counted every hour, and the moths on the sticky traps were recorded. The distribution of the treatments was randomized within six replicate series, using a total of 42 traps.

Data analyses

The statistical analyses were performed using the SPSS 19.0 statistical software package (SPSS Inc., Chicago, IL, USA). Analyses of variance (ANOVA) and Duncan's multiple range test were used to assess the effect of age on the time spent calling. The percentages of moths calling, wind tunnel and copulation results were analyzed using Tukey's Honestly Significantly Different (HSD) tests of arcsine-transformed data. The data on the number of moths captured in the field were analyzed using nonparametric Friedman test analysis of variance followed by Bonferroni corrections. The level of significance in all tests was set at 0.05.

Table 1. Percentage (%) of females of *Monema flavescens* of different ages recorded calling at different times after the onset of the scotophase.

Scotophase (h)	Percentage of *Monema flavescens* females calling (%, mean ± SE)					
	1-day old	2-day old	3-day old	4-day old	5-day old	6-day old
D0~1	0.0 ± 0.0b	0.0 ± 0.0c	0.0 ± 0.0d	0.0 ± 0.0d	4.5 ± 2.2d	2.2 ± 2.2b
D1~2	0.0 ± 0.0b	0.0 ± 0.0c	0.0 ± 0.0d	15.6 ± 8.0d	17.8 ± 2.2bcd	13.3 ± 5.1ab
D2~3	0.0 ± 0.0b	10.0 ± 5.8bc	16.7 ± 8.4d	62.2 ± 6.7bc	42.2 ± 5.9abcd	32.2 ± 9.1ab
D3~4	2.2 ± 2.2b	31.1 ± 5.9b	55.5 ± 2.2bc	78.9 ± 2.9ab	53.3 ± 7.7ab	41.1 ± 10.6a
D4~5	7.8 ± 4.8ab	64.5 ± 9.1a	81.1 ± 1.1a	91.1 ± 4.0a	60.0 ± 9.6a	41.1 ± 9.7a
D5~6	17.8 ± 4.5a	61.1 ± 4.8a	70.0 ± 6.7ab	75.6 ± 10.6ab	52.2 ± 10.6abc	36.7 ± 8.8ab
D6~7	2.2 ± 1.1b	21.1 ± 1.1bc	44.5 ± 6.2c	30.0 ± 8.8cd	32.2 ± 8.0abcd	22.2 ± 6.2ab
D7~8	3.3 ± 3.3b	3.3 ± 3.3c	14.4 ± 2.9d	11.1 ± 4.0d	16.6 ± 6.7cd	6.7 ± 1.9ab
D8~10	1.1 ± 1.1b	2.2 ± 2.2c	6.7 ± 1.9d	1.1 ± 1.1d	5.6 ± 2.9d	2.2 ± 1.1b

There were three replicates of each of the observations throughout the scotophase (N = 30). The different letters within columns indicate significant differences at P ≤ 0.05 according to Tukey's HSD of arcsine-transformed data.

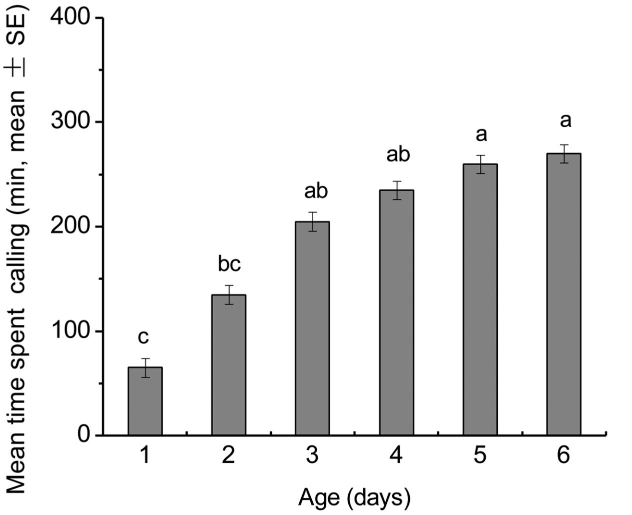

Fig. 2. The mean time females of *Monema flavescens* of different ages spent calling in the scotophase. Values are means (± SE). Values followed by different letters are significantly different (P ≤ 0.05) based on Duncan's multiple range test.

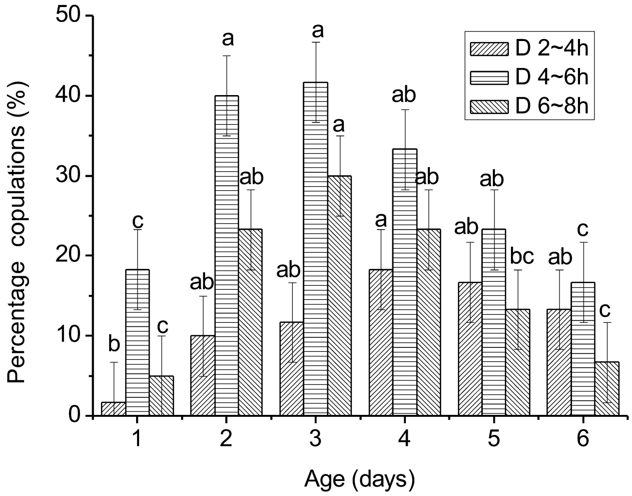

Fig. 3. The percentage of *Monema flavescens* of different ages recorded mating at different times after the onset of the scotophase. Values are means (± SE). Values followed by different letters are significantly different (P ≤ 0.05) based on Tukey's HSD of arcsine-transformed data.

RESULTS

Calling behaviour

Calling behaviour of females of *M. flavescens* of different ages was recorded at different times during the scotophase (Table 1). Females of *M. flavescens* were only sexually active during the scotophase. Calling activity of 1 day old females (1 day old) started 3 h after the onset of the scotophase, and the mean time of the onset of calling occurred earlier as they increased in age. The 5 to 6 day old females called throughout the scotophase. Only 34.5% of the females called on the night (1 day old) after emergence, whereas almost all females (97.8%) called on the next night (2 day old) (Fig. 1). The percentage of females calling significantly declined on the 5th night after emergence when about 66.7% of females called. The mean time spent calling increased significantly with age (Fig. 2).

Wind tunnel experiments

The first weak response of *M. flavescens* males to the sex pheromone occurred on the night after emergence and the peak response on the third night (Table 2). Males responded to the pheromone throughout the scotophase, but the peak response occurred 4 to 6 h after the onset of the scotophase (Table 3).

Table 2. Effect of age on response (%) of *Monema flavescens* males to pheromone extracts in a wind tunnel.

Age (days)	Response of *Monema flavescens* males (%, mean ± SE)			
	Take off	Directed flight	Landing	Copulation attempts
1	53.3 ± 3.8c	33.3 ± 3.8c	17.8 ± 2.2d	13.3 ± 0.0d
2	84.4 ± 5.9bc	73.3 ± 3.8b	35.5 ± 2.2cd	31.1 ± 2.2cd
3	100.0 ± 0.0a	95.5 ± 2.2a	80.0 ± 3.9a	75.5 ± 2.2a
4	97.8 ± 2.2ab	91.1 ± 2.2ab	73.4 ± 6.7ab	66.7 ± 6.7ab
5	93.3 ± 3.8ab	86.7 ± 3.8ab	55.5 ± 2.2bc	51.1 ± 2.2bc
6	86.7 ± 3.8b	75.5 ± 2.2b	44.4 ± 5.9c	35.6 ± 4.4c

The different letters within columns indicate significant differences at P ≤ 0.05 according to Tukey's HSD of arcsine-transformed data.

Copulation

M. flavescens was only observed copulating during the scotophase. Copulations were first recorded at the beginning of the second hour and reached a peak about 4 to 6 h into the scotophase (Fig. 3). The percentage mating was significantly dependant on the age of the virgin females. The percentage was highest for 3 day old moths (41.7%), followed by 2 day old (40%), 4 day old (33.3%), 5 day old (23.3%), 1 day old (18.3%), and 6-d-old (16.7%). The average duration of copulation was 120.8 ± 12.6 min (mean ± SE; N = 20) and ranged from 60 to 240 min.

Field tests

Unbaited traps set during the scotophase and traps baited with virgin female set during the photophase failed to attract males of *M. flavescens* in the field. Traps baited with 2 day old and 3 day old virgin females captured more males than the other traps (Table 4). The number of males captured significantly depended on the age of the virgin females and the time from the onset of the scotophase. Most males were captured in traps 4 to 6 h (1 to 2 day old fe-

Table 3. Effect of time after the onset of the scotophase on the response (%) of *Monema flavescens* males to pheromone extracts in a wind tunnel.

Hour of scotophase	Response of *Monema flavescens* males (%, mean ± SE)			
	Take off	Directed flight	Landing	Copulation attempts
0~2	44.5 ± 11.8b	33.3 ± 3.8b	13.3 ± 3.8c	6.7 ± 3.8b
2~4	77.8 ± 4.5b	64.3 ± 5.9b	40.0 ± 3.8b	31.1 ± 5.9b
4~6	100.0 ± 0.0a	93.3 ± 3.8a	77.8 ± 4.5a	71.1 ± 5.9a
6~10	73.3 ± 7.7b	62.2 ± 5.9b	37.8 ± 2.3b	28.9 ± 2.2b
8~10	33.3 ± 5.9c	28.9 ± 3.8c	13.3 ± 2.2c	6.7 ± 5.9b

The *Monema flavescens* males tested were 3 days old (N = 45). The different letters within columns indicate significant differences at P ≤ 0.05 according to Tukey's HSD of arcsine-transformed data.

Table 4. Effect of the photophase and the time after the onset of the scotophase on catches of male *M. flavescens* in traps baited with 1 to 6 day old virgin females.

Photophase (L) Scotophase (D) (h)	Males captured / trap (mean ± SE)						
	1-day old	2-day old	3-day old	4-day old	5-day old	6-day old	Not baited
L0~14	0.0c	0.0d	0.0d	0.0a	0.0c	0.0b	0.0
D0~1	0.0c	0.0d	0.0d	0.0a	0.0c	0.0b	0.0
D1~2	0.0c	0.0d	0.0d	0.0a	0.3 ± 0.5abc	0.3 ± 0.5ab	0.0
D2~3	0.0c	0.0d	0.0d	0.7 ± 0.5a	1.8 ± 1.5a	0.8 ± 0.7a	0.0
D3~4	0.3 ± 0.5abc	1.2 ± 0.7bc	2.3 ± 1.7ab	2.3 ± 2.1a	1.3 ± 1.2abc	0.3 ± 0.5ab	0.0
D4~5	1.5 ± 1.0a	3.5 ± 1.8a	3.2 ± 1.6a	2.0 ± 2.2a	0.5 ± 0.5abc	0.0b	0.0
D5~6	1.2 ± 1.2ab	2.2 ± 1.4ab	1.2 ± 0.7bc	0.8 ± 1.2a	0.2 ± 0.4bc	0.0b	0.0
D6~7	0.7 ± 0.8abc	0.8 ± 0.7bcd	0.3 ± 0.5cd	0.0a	0.0c	0.0b	0.0
D7~10	0.0c	0.0d	0.0d	0.0a	0.0c	0.0b	0.0
Total	3.7 ± 1.4ab	7.7 ± 2.1a	7.0 ± 1.9a	5.8 ± 1.5ab	4.1 ± 2.7ab	1.4 ± 2.0b	0.0

Means in a column followed by different letters are significantly different after Bonferroni correction (1 day old: H = 30.5, d.f. = 8, P = 0.000; 2 days old: H = 38.9, d.f. = 8, P = 0.000; 3 days old: H = 38.0, d.f. = 8, P = 0.000; 4 days old: H = 29.7, d.f. = 8, P = 0.000; 5 days old: H = 27.7, d.f. = 8, P = 0.001; 6 days old: H = 21.5, d.f. = 8, P = 0.006).

males), 3 to 5 h (3 to 4 day old) and 2 to 4 h (5 to 6 day old) after the onset of the scotophase (Table 4).

DISCUSSION

Female calling, male responsiveness and mating behaviour of *M. flavescens* had a distinct diel periodicity. Under natural conditions, 34.5% of the females that called during the first night were fertilized that night, the number of females calling on the second night was 97.8%, and the number of females older than 2 days recorded calling was almost zero. These results indicate that most female moths were sexually mature on the second night. One day old females started calling 3 h after the onset of the scotophase, but 5 to 6 day old females called during the first hour of the scotophase. The result that females began calling earlier during the scotophase and for a longer time as they aged is in agreement with that recorded for several other species of moths (Seol et al., 1986; Delisle, 1992; Spurgeon et al., 1995; Mazor & Dunkelblum, 2005). Older females advance their calling time to increase their mating success relative to younger females, otherwise they would be at a disadvantage compared to the younger females if they did not spend more time calling (Delise, 1995; Xiang et al., 2010; Liu, 2013).

Wind tunnel and copulations tests indicate that the males were sexually mature on the third night, one day later than female moths. This accounts for why most 2 day old females called but were less likely to be mated than 3 day old females. Similar results are reported for the insect tomato looper, *Chrysodeixis chalcites* (Snir et al., 1986).

Field tests indicate that none of the traps caught male moths during the day, but were most attractive 4 to 6 h (1 to 2 day old), 3 to 5 h (3 to 4 day old) and 2 to 4 h (5 to 6 day old) after the onset of darkness, respectively. These results also indicate that the diel periodicity in calling conform with the result of the field tests, and similar results are reported for *Maruca vitrata* (Lu et al., 2007) and *Isoceras sibirica* (Lu et al., 2013).

The calling and mating in Lepidoptera have a certain rhythm. Studying the rhythm of their reproductive behaviour can provide an important theoretical basis for the effective control of insects and reducing the economic losses they cause. However, the effects of some other factors such as temperature and photoperiod should also be studied in the future.

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