Emergence and Reproductive Rhythm of *Clostera anastomosis* (Lepidoptera: Notodontidae)[1]

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Abstract *Clostera anastomosis* L. (Lepidoptera: Notodontidae) is a serious defoliator of poplar, *Populus* spp., trees in China. To establish a baseline of information for possible ecological management of this pest, we studied its emergence, courtship, mating, and oviposition behaviors in the laboratory at 27 ± 1°C and 60 ± 10% relative humidity under a 14:10-h (light:dark) photoperiod. Under these conditions, peak emergence of female adults occurred in the sixth day after pupation, and peak emergence of males was in the seventh day after pupation. Emergence for both sexes occurred throughout the day. Courtship behavior began at the sixth hour of scotophase, reaching peak activity between the 10th hour of scotophase and the first hour of photophase. The courtship and mating success rate were highest for 1-d-old females, and then gradually decreased with age until no mating was observed after females were 4 d old. With 1-d-old females, mating was only observed from the seventh hour of scotophase to the first hour of photophase, with peak activity at 0.5 h after the onset of photophase. Oviposition primarily occurred within 3 d after mating, with 49.8% of the eggs being deposited during the first day after mating. These results demonstrate that there are distinct circadian rhythms in adult emergence and subsequent reproductive behavior of *C. anastomosis*, thus providing a basis for development of monitoring and management strategies of this pest.

Key Words *Clostera anastomosis*, adult emergence, courtship behavior, mating behavior, oviposition behavior

Clostera anastomosis L. (Lepidoptera: Notodontidae) is widely distributed in China, Japan, North Korea, Russia, Mongolia, and some European countries. In China, *C. anastomosis* is mainly distributed in northeastern and northern China, Zhejiang, Jiangsu, and other areas, where it is an important foliage-feeding pest of poplar (*Populus* spp.) and willow (*Salix* spp.) (Liu et al. 2010, Wu and Fang 2003). In recent years, poplar tree cultivation has continuously expanded, and *C. anastomosis* damage has become a serious problem in reducing aesthetic beauty of urban areas, compromising landscape ecology, and causing certain economic losses (Fang et al. 2007, Li et al. 2000, Wang 2016, Wu et al. 2006). Studies have reported the biological characteristics and control techniques of *C. anastomosis* (Zhang 2016); however, adult emergence and reproductive behavior have not been

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reported and could prove important in the development of strategies and tactics basic to effective management of the pest. Its control remains based on the use of chemical insecticides (Fang et al. 2007, Liu 2015, Yang et al. 2004, Zhou et al. 2010, 2011). Management using plant-derived insecticides (Chen 2014, Chen et al. 2007, Fang 2013, Fang et al. 2017, Li et al. 2013), microbial agents (Ge et al. 2014, Huang et al. 2007, Li et al. 2011, Yang and Lin 2000, Yin 2020, Yin et al. 2015), and insect pheromones (Wang et al. 1999) has not been thoroughly investigated.

Insect metabolism, polymorphism, dormancy, emergence, reproduction, and other growth and behavior activities are largely impacted and controlled by circadian rhythms. Changes in circadian rhythms can directly affect the interspecific competition and synchronized mating of insects, thereby ensuring the reproductive isolation of similar species (Giebultowicz 2000). There are many factors, for example, temperature, humidity, food, population density, etc., that can affect insect circadian rhythms. Perhaps the most important of the abiotic regulatory factors is light (Fónagy 2009). At present, there are no reports on the circadian rhythm of *C. anastomosis*, and there are relatively few studies on the behavioral rhythm of the Notodontidae, with the exception of *Thaumetopoea pityocampa* (Denis & Schiffermüller) (Frérot and Malosse 1990, Paiva and Zhang 1998), *Clostera anachoreta* Denis & Schiffermüller (Liu et al. 2009, Wang and Tan 2010, Zhang 2007), and *Micromelalopha troglodyta* (Graeser) (Chen et al. 2014; Fan et al. 2014, 2015).

Knowledge of insect circadian rhythm aids in efficacious targeting of management strategies and tactics (e.g., monitoring, trapping, sex pheromone usage, etc.) to prevent and control pest populations. In integrated pest management, knowledge of pest behavior is a basis for pest prevention and control. Our objective in this study was to define the circadian rhythm of *C. anastomosis* related to adult emergence and reproductive behavior in order to provide a theoretical reference for prediction of population outbreaks, defining the population dynamics of the insect, and determining the time periods for effective monitoring and management strategies.

Materials and Methods

Insect. *Clostera anastomosis* larvae were collected from poplar trees growing in stands near Yongxiu County, Jiujiang City, Jiangxi Province, China, and transported to the laboratory where they were reared on fresh poplar leaves in circular containers (diameter 25 cm, height 15 cm). Once the larvae pupated, the date was recorded and larvae were placed individually in petri dishes in an environmentally controlled room maintained at 27 $\pm$ 1°C and a relative humidity (RH) of 60 $\pm$ 10% with a photoperiod of 14:10-h (light:dark [14L:10D]). A source of 10% (w/v) sucrose was provided as food for emerging adults.

Eclosion. Initially each pupa was observed at 9:00 a.m., 3:00 p.m., and 9:00 p.m. daily until an adult emerged. We then observed each pupa each hour thereafter until all pupae had emerged. The time of emergence for each was recorded.

Courtship behavior. Ninety adult females were randomly selected from those emerging from the pupae and placed individually in plastic cups (11-cm height, 8-

cm top diameter, 5-cm bottom diameter). Each cup was inverted onto a bottom of a petri dish containing a supply of 10% sucrose. Moths were collected and placed in cups within 24 h of emergence. Each moth was observed for characteristic calling behavior of courtship (e.g., protruding yellow-colored sex glands from the abdomen) every 30 min from 5 h from the end of the dark phase to 9 h into the light phase daily for 7 d. Moths were observed under weak red light to avoid disturbing the courtship behavior.

Mating behavior. Fifteen pairs of male and female adult moths that emerged on the same day were placed in a cage (50 × 50 × 50 cm), with a total of three concurrent replicates (cages). The number of mating pairs and the duration of the mating activity were recorded every 30 min until the death of the moths. The time of observation was from 6 h into the dark phase until 2 h into the next dark phase.

Oviposition. Mated females from the previous mating observations were placed individually in the plastic cups and inverted on a petri dish bottom as previously described. Ten females comprised a replicate, with three replicates. Each night at 9:30 p.m., we counted the number of eggs that had been deposited by each female over the past 24 h. Each female was then placed in a clean cup and inverted on a clean petri dish. Daily observations and counts were made until all females had expired.

Statistical analysis. Statistical analyses were performed using the analysis of variance procedure of the IBM SPSS Statistics 26 for Windows (SPSS Inc., Chicago, IL). The Tukey test of significance was used to determine differences ($P < 0.05$) among treatment means.

Results

Eclosion. We observed a total of 262 *C. anastomosis* adults that emerged in 1 d from pupae held at 27 ± 1°C, 60 ± 10% RH, and a photoperiod of 14L:10D. Of those, 127 were females and 135 were males. Moths emerged throughout the day, but mainly during the period from 11 h into the light period to 4 h into the dark period. The greatest number ($n = 40$, 29.6%) emerged at 14 h into the light period. Females emerged during the period from 12 h in the light period to 5 h into the dark period, with peak emergence at 1 h into the dark period (Fig.1).

Under the same conditions, we counted a total of 566 moths that emerged over the 10-d period of observation. Of these, 231 were females and 335 were males. Both males and females began to emerge on the fifth day after pupation. The peak emergence of females occurred on the sixth day after pupation when 139 females (60.2% of the total) emerged. Female emergence decreased rapidly thereafter until the ninth day, when no female emergence was observed. Male emergence peaked 7 d after pupation when we observed 203 males emerging. No males emerged after 10 d (Fig. 2).

Courtship behavior. We observed female courtship in the form of calling behavior (e.g., extrusion of the yellow-colored sex glands from the abdomen) during the period of darkness (Fig. 3). Calling behavior began between 5 and 6.5 h into the dark period and continued until 9 h into the subsequent light period. Peak courtship activity (e.g., number of females exhibiting calling behavior) was observed between 10 h into the dark period until 1 h into the light period.

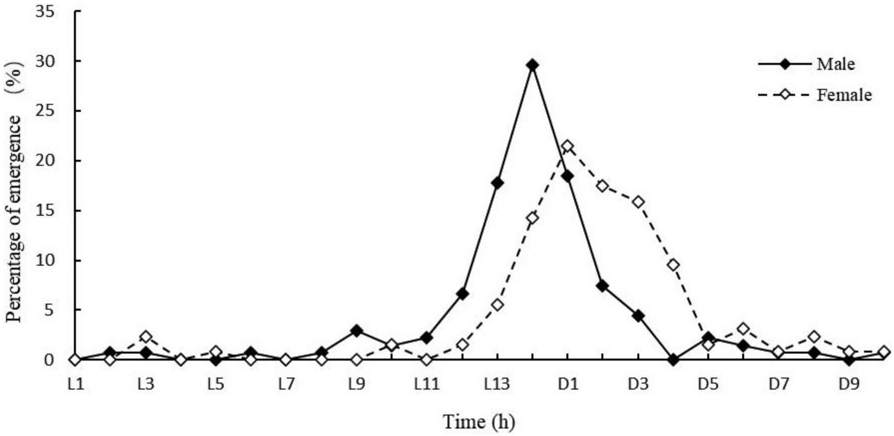

Fig. 1. Circadian rhythm of emergence of *C. anastomosis* (L: photophase; D: scotophase).

Females were observed to exhibit calling behavior the day of emergence from pupation (Fig. 3), but the greatest percentage of females exhibiting calling behavior occurred on 1 (97.8%) and 2 d (60.0%) after emergence (Fig. 3). The females can have courtship behavior on the day of emergence, when the highest courtship rate was 97.8%, and the courtship rate dropped to 60.0% at 2 d of age. At 7 d, the percentage showing calling behavior was 44.4%.

With respect to start and termination times of courtship behavior, 1-d-old females began calling 9.5 h into the dark period (0.5 h before light), 2-d-old females began calling 9 h into darkness, 3- to 4-d-old females began calling at 7 h into the darkness, and 5- to 7-d-old females began 6 h into darkness. Thus, the average start time of female calling gradually advanced with increasing age of the females.

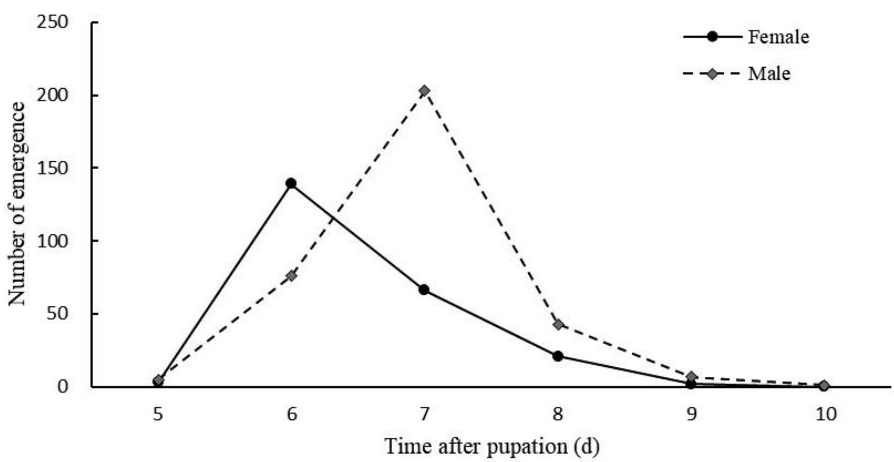

Fig. 2. Rhythm of emergence of *C. anastomosis* during 24-h period.

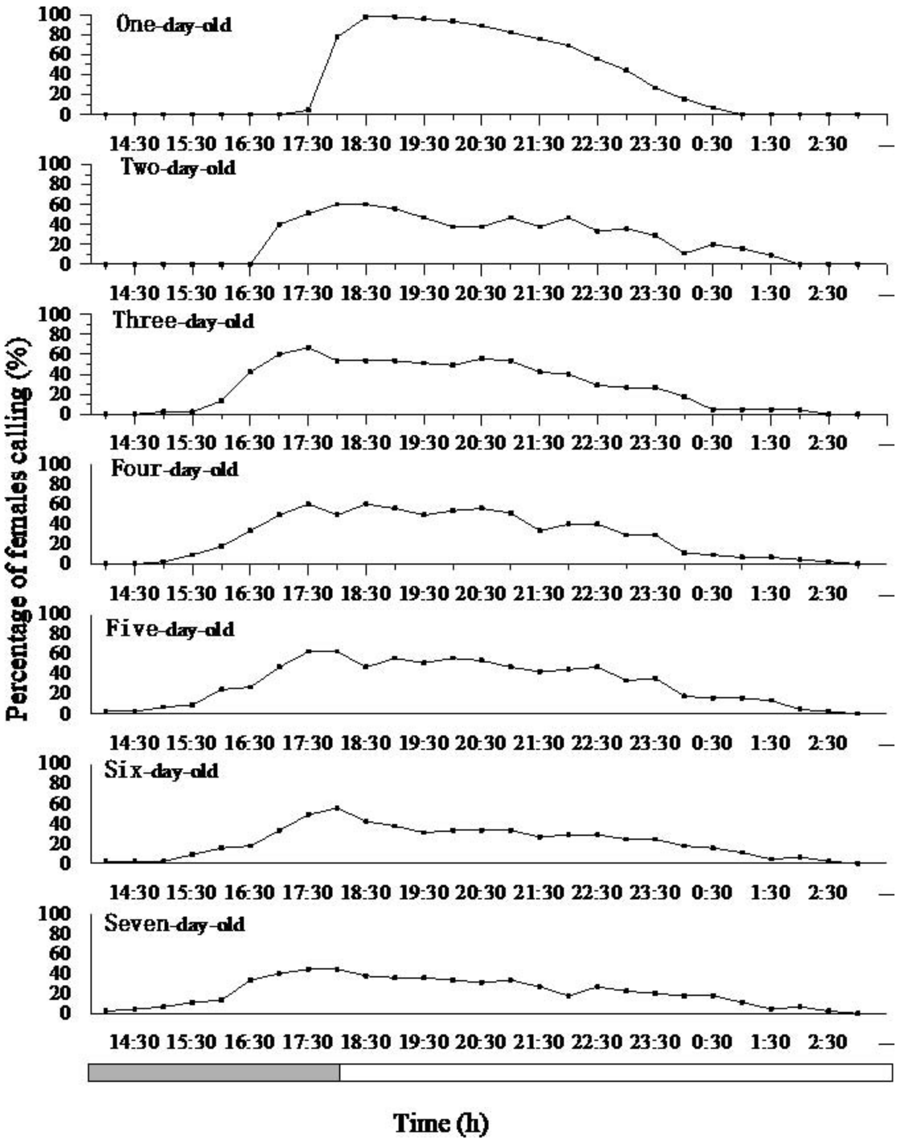

Fig. 3. Percentage of female *C. anastomosis* calling at different ages and at different time into the scotophase.

Calling was terminated 6.5–8.5 h into the light period regardless of age of the female moths.

The average duration of calling behavior did not significantly differ among the different ages of females (Table 1). The duration (mean ± SD) ranged from 3.50 ± 0.71 d (6 d after emergence) to 5.51 ± 0.26 d (5 d after emergence). The mean

Table 1. Mean ± SD duration and frequency of calling of female *C. anastomosis* of different ages.*

Age (d)	Duration of Calling (h)	Frequency of Calling (number/h)
1	5.28 ± 0.72a	1.20 ± 0.10b
2	3.93 ± 0.86a	2.13 ± 0.23a
3	4.70 ± 0.45a	1.93 ± 0.12a
4	5.05 ± 0.38a	1.97 ± 0.07a
5	5.51 ± 0.26a	2.33 ± 0.23a
6	3.50 ± 0.71a	2.07 ± 0.23a
7	3.89 ± 0.74a	1.70 ± 0.10ab

* Means within rows followed by different lowercase letters for each age are significantly different at the 0.05 level (Tukey test).

frequency of calling behavior was significantly lower in 1-d-old females in comparison to females 2, 3, 4, 5, and 6 d old (Table 1).

Mating. Under the temperature, RH, and photoperiod conditions of this study, almost no copulating adults were observed 3 to 7 h into the dark period (Fig. 4). Beginning at 8 h into darkness, the mating rate gradually increased to reach a peak in activity at 2 h into the light period when 76.2% of the pairs were mating. Mating was observed starting at 7 h into darkness and ended 13 h into the light period (Fig. 5). Of the moths observed, 59.0% started mating as the light period began; no mating was initiated 1 h into the light period. Males and females started to separate 12 h into the light period, and 81.2% of adults terminated mating activity 0.5 h into darkness. All mating adults had terminated the activity by 2 h into darkness. It is apparent from these results that the mating behavior of *C. anastomosis* is a long continuous process.

Under these laboratory conditions, 75.6% of 1-d-old adults were engaged in mating. After that, the mating activity gradually decreased with the age, with 13.3% of 2-d-old adults mating, 4.4% 3-d-old adults mating, and no mating observed after adults were 3 d old (Table 2). As the age of the adults increased, the duration of mating duration was increased: at 1 d old mating duration was 14.0 ± 0.1 h, at 2 d old it was 15.3 ± 0.1 h, and 3 d old it was 16.5 ± 0.2 h.

Oviposition. The peak time for oviposition of mated females was the first day after mating when 49.8% of mated females deposited their eggs. The percentage ovipositing decreased to 19.8% on the second day, 9.8% on the third day, and then gradually decreased until the ninth day when 61.5% of females no longer laid eggs. Only a very small number of females were observed to lay eggs for up to 13 d. Percentage of females laying eggs differed significantly among the ages (Fig. 6). The number of eggs (mean ± SD) laid by the mating females was 291.9 ± 40.4 ($n=30$). The number of eggs laid by females in the first 3 d after mating accounted for 79.4% of the total eggs oviposited in the lifetime of the females.

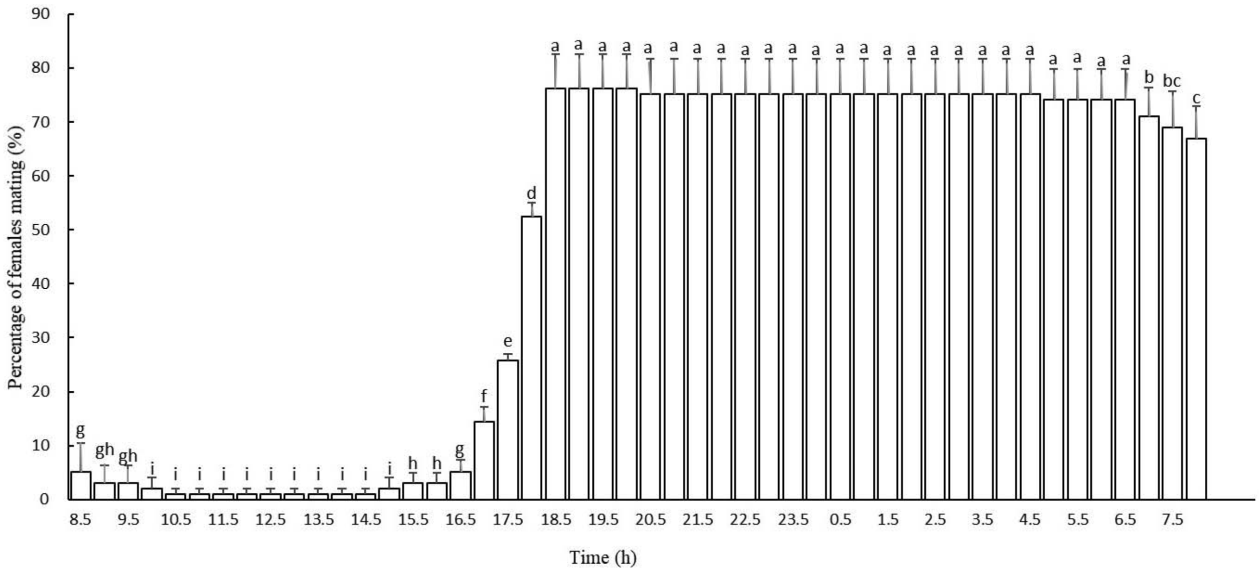

Fig. 4. Percentage of *C. anastomosis* mating at different times. Data are mean $\pm$ SD; bars with different lowercase letters for each age are significantly different ($P = 0.05$; Tukey test).

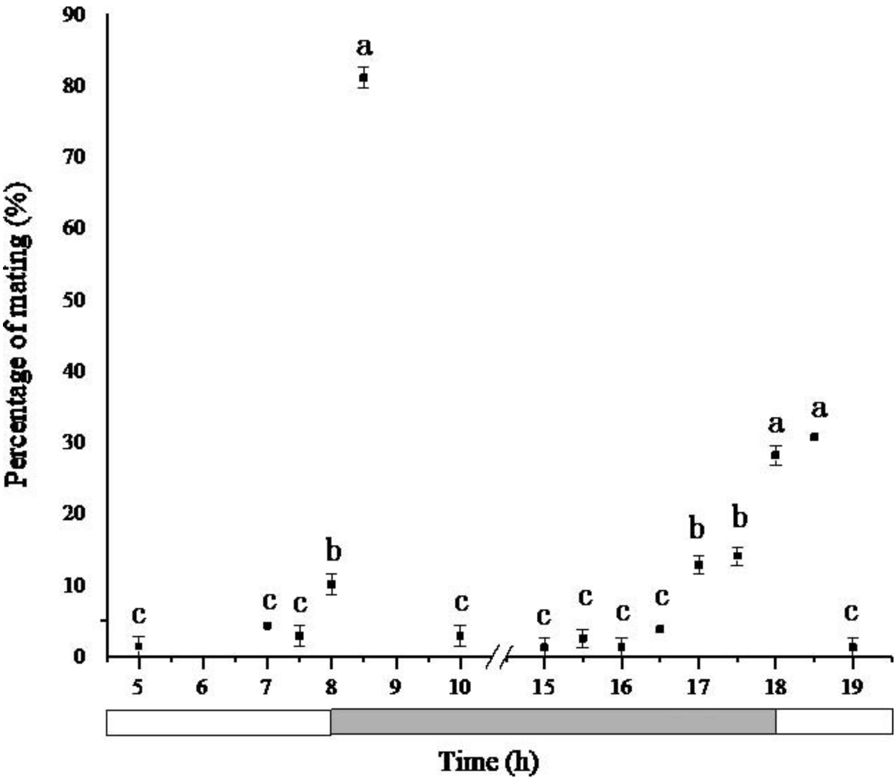

Fig. 5. Percentage of *C. anastomosis* pairs mating at the beginning and the end of different time periods. Data are mean ± SD; bars with different lowercase letters for each age are significantly different ($P = 0.05$; Tukey test).

Table 2. Mean ± SD mating percentage and duration of mating of female *C. anastomosis* of different ages.*

Age (d)	Mating Percentage (%)	Duration of Mating (h)
1	75.56 ± 2.22a	14.0 ± 0.07a
2	13.33 ± 3.85b	15.3 ± 0.07b
3	4.44 ± 2.22c	16.5 ± 0.20c
4	0.00 ± 0.00c	—
5	0.00 ± 0.00c	—

* Means within rows followed by different lowercase letters for each age are significantly different at the 0.05 level (Tukey test).

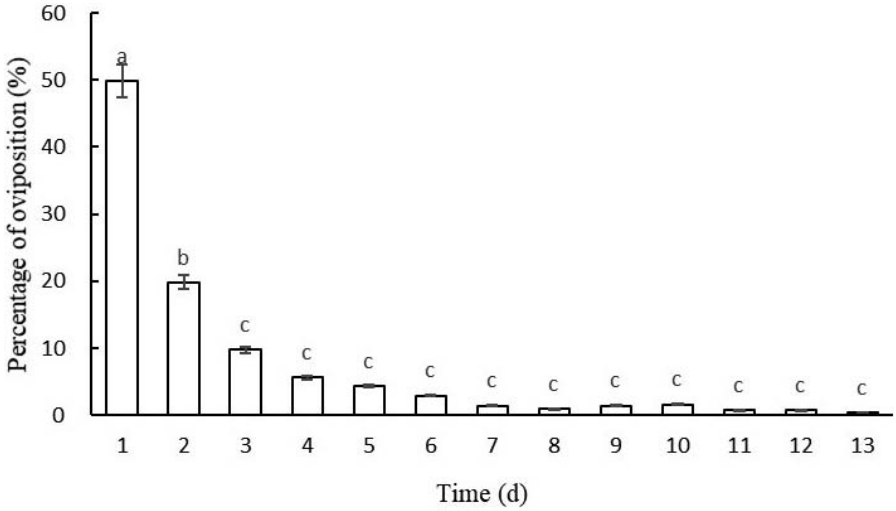

Fig. 6. Percentage of female *C. anastomosis* ovipositing at different times following mating. Data are mean ± SD; bars with different lowercase letters for each age are significantly different ($P = 0.05$; Tukey test).

Discussion

Our results showed that, under the laboratory conditions of 27 ± 1°C, 60 ± 10% RH, and a photoperiod of 14L:10D, *C. anastomosis* females emerge from pupation 1 d earlier than males when the pupae enter pupation on the same day. This phenomenon has been reported with other lepidopteran species, such as *Ephestia kuehniella* Keller (Pyralidae) (Xu et al. 2008), *Metisa plana* Walker (Psychidae) (Rhainds et al. 1999), and *Spodoptera exigua* (Hübner) (Noctuidae) (Li et al. 2008). To the contrary, males of other lepidopteran species, such as *Heortia vitessoides* Moore (Crambidae), emerge before females (Wang et al. 2018). Such temporal differences in emergence of the sexes may be an evolutionary mechanism to reduce genetic inbreeding (Rhainds et al. 1999). When males and females of *C. anastomosis* that pupated on the same day emerge on the same day, *C. anastomosis* males emerged earlier in the day than females, which is contrary to earlier reports of *C. anachoreta* eclosion patterns (Liu et al. 2009). Perhaps this is because most of the females that pupated on the same day have already emerged the day before most of the males, thus, the males emerge earlier in the day than the females, which can increase mating success rate.

Under these same conditions, we found that most females initiated courtship (e.g., calling behavior) immediately after eclosion. The highest courtship and mating activities of females occurred 1 d after emergence and gradually declined thereafter. On those days, the courtship peaks occurred primarily in the dark period beginning at 10 h into darkness and continuing to 1 h into light. Peak mating activity was at 0.5 h into the light period. On occasion, both courtship and mating continued into the next dark period. Liu et al. (2009) and Zhang (2007) reported similar results with *H. vitessoides*; however, most studies report courtship and mating of lepidopterans occurring only in the dark period, e.g., *Agrotis ipsilon* (Hufnagel) (Qiao et al. 2018), *Micromelalopha troglodyte* (Graeser) (Fan et al. 2014, Fan et al. 2015), *Lasiognatha cellifera* Meyrick (Chang et al. 2015), *H. vitessoides* (Wang et al. 2018), *Atrijuglans hetaohei* Yang (Nan et al. 2017), *Orthaga achatina* (Butler) (Wang et al. 2009), *Kumasia kumaso* (Sugi) (Shu et al. 2012), and others. Differences in insect courtship and mating times are important mechanisms of reproductive isolation among closely related species (Shi and Zhao 1986).

The synthesis and release of sex pheromone in most moths coincides with the timing of the female courtship behavior, such as reported with *Plecoptera oculata* Moore (Cao et al. 2018), *Zeuzera leuconotum* Butler (Liu et al. 2013), and *S. exigua* (Li et al. 2008, Dong and Du 2001). Thus, the peak period of sex pheromone synthesis and release should coincide with observed peak calling activity by female moths. This can be used to predict the optimum time for use of sex pheromone in insect management tactics and strategies.

Insect courtship and mating behavior can differ among species, and both are closely linked to age of the moths. While the courtship and of *C. anastomosis* peaked after 1 d of emergence, other lepidopteran species exhibit calling and mating activity peaks 2 to 3 d after eclosion (Cao et al. 2018, Henneberry and Clayton 1985, Liu et al. 2013, Lu et al. 2007). Initiation of calling behavior by *C. anastomosis* females gradually advances with increased age of the moths. This same phenomenon has been reported in a number of lepidopterans representing different taxonomic families, for example, *Crocidosema aporema* (Walsingham) (Tortricidae) (Altesor et al. 2010), *Zamagiria dixolophella* Dyar (Pyralidae) (Castrejón-Gómez 2010), *Autographa gamma* L. (Noctuidae) and *Cornutiplusia circumflexa* (L.) (Noctuidae) (Mazor and Dunkelblum et al. 2005), and *Lonomia obliqua* Walker (Saturniidae) (Zarbin et al. 2007). Swier et al. (1977) postulated that older virgin female moths could increase their ability to compete with young virgin moths by advancing the courtship start time. Furthermore, the peak of mating activity follows that of the calling behavior, indicating that the courtship activity of females is an important factor affecting the success of mating in *C. anastomosis*.

In summary, our results from this laboratory study provide a base of information that will prove useful in understanding the biological and behavioral rhythms of *C. anastomosis*. These results also provide important information on sex pheromone production and release by *C. anastomosis* females, which provides a reliable basis for determining optimal times for manual extraction of the sex pheromone, as well as initiation of monitoring or trapping using the pheromone, or pheromone-based or biologically based management tactics for this pest.

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