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Flying males mediate oviposition and migration in female *Mythimna separata* (Lepidoptera: Noctuidae)

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Research Paper

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Abstract

In recent decades, the oriental armyworm, *Mythimna separata* (Walker), has caused severe damage to staple grains in China. However, little is known about when *M. separata* begin their first migration and the role of males in reproduction and migration. Here, the migratory benefits and reproductive costs of flight frequency were examined in adults under laboratory conditions. We found that flying males had a positive effect on ovarian and reproductive development in females who flew for 1–2 nights by comparing two treatment groups (flying and nonflying male groups). Moreover, flying males decreased the flight capacity and flight propensity of females. In contrast, flight for more than two nights by males significantly inhibited ovarian and reproductive development in adult females. Compared with the controls (0 night), male flight for 1–2 nights significantly shortened the preoviposition period but significantly increased ovarian and reproductive development in females. However, male flight for more than three nights significantly inhibited female reproduction and flight capacity. These results indicate that *M. separata* begin their first migration within 2 days after emergence and fly for two nights. Prolonged flight times can result in significant reproductive costs. Females initiated their first migration earlier than males due to a stronger flight capacity. These observed findings will be useful for forecasting and monitoring population dynamics to prevent outbreaks of *M. separata* and reduce crop losses.

Introduction

The oriental armyworm, *Mythimna separata* (Walker) (Lepidoptera: Noctuidae), is a major cereal crop pest in Asia and Australian countries (Sharma and Davies, 1983; Lee and Uhm, 1995; He *et al.*, 2017). Due to its typical seasonal behaviour of long-distance migration, generalist food habits, fast reproduction, high fecundity and strong adaptability (Li *et al.*, 1964; Li, 1996; Wang *et al.*, 2006; Jiang *et al.*, 2011), *M. separata* has been considered a major biological challenge in China in recent decades (Zeng *et al.*, 2013; Jiang *et al.*, 2014*a*). Additionally, due to global climate change, current crop structures and farming systems, and the adaptability of *M. separata*, the patterns of overwintering and outbreaks are changing, resulting in a significant decline in forecasting for prevention and control effects (Zhang *et al.*, 2012; Jiang *et al.*, 2014*b*; Zhao and Cheng, 2016). Therefore, it is essential to elucidate and understand the mechanisms of migration and outbreaks to improve the accuracy of forecasting for the prevention and sustainable management of *M. separata* in the future and reduce the use of pesticides to protect the environment.

From an evolutionary perspective, insect migration is considered a life-history strategy to leave a habitat incompatible with development and relocate to an adequate breeding environment (Drake *et al.*, 1995; Drake and Reynolds, 2012; Chapman *et al.*, 2015). Evidence of this theory is provided by previous studies on migratory pests of field crops, such as *Mythimna separata* and *Agrotis ipsilon*, both of which complete long-range migrations (Chen *et al.*, 1989; Johnson, 1995; Jiang *et al.*, 2011). Recently, Sappington (2018) has demonstrated that migratory flight behaviour is characterized as non-appetitive and fundamentally differs from proximate or local search behaviours. However, after the termination of migratory flight by an internal circadian rhythm (the onset of dusk or dawn) or endogenous signals (Compton, 2002), migratory insects rapidly search for potential resources such as food and suitable habitats for successful breeding (Dingle, 2014; Sappington, 2018).

It is generally thought that migrants in insects have greater reproductive potential that is passed on to the next generation than non-migrants; thus, it results in migrants investing more resources in reproduction than non-migrants (Chapman *et al.*, 2015), similar to migrating birds and mammals (Sibly *et al.*, 2012; Stevens *et al.*, 2014). Prior studies have shown that there exists a trade-off between migration and reproduction in migratory insects when considering their limited internal resources (Johnson, 1969; Rankin *et al.*, 1986). The

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interaction relationship between migration and reproduction is not fixed, which differs from species to species, flight stage and other factors (Zhang *et al.*, 2015). Some studies have verified that sex, age and juvenile hormone (JH) may affect the flight capacity and reproduction of adult insects, thereby altering the larval density of the offspring (Luo *et al.*, 2001; Cheng *et al.*, 2012; Zhang *et al.*, 2020).

The onset of migratory behaviour is generally initiated by sexually immature adults for a variety of migratory noctuid species (Gatehouse and Zhang, 1995). The migration process usually involves long-range dispersal of sexually immature females, subsequent ovarian development and mating at the end of migration in the Noctuidae (Rhainds, 2010). Similar patterns have been reported in redbacked cutworms, *Euxoa ochrogaster* and some other noctuid species (Gerber and Walkof, 1992; Coombs *et al.*, 1993), with a high proportion of mated females among migrant individuals with mature oocytes. Zhao *et al.* (2009) has also demonstrated both ovarian development and mating of *M. separata* females occur towards the end of the migratory phase, and the completion of migration takes a series of days rather than one continuous flight.

To date, many studies have been conducted in *M. separata* to explore the occurrence and regularity of migration, reconstruct migratory pathways, and develop monitoring and forecasting techniques using many tools, including radar observation, searchlight traps, flight mill experiments and trajectory analysis models (Chen *et al.*, 1989; Feng *et al.*, 2008; Jiang, 2018; Zhang *et al.*, 2018). However, little is known about the effects of males on reproduction and flight initiation in *M. separata*. In this study, we investigated flight activity, flight capacity and other flight-related physiological results through a flight mill system (Kim *et al.*, 2010; Rovnyak *et al.*, 2018). Our objectives were to evaluate the role of males participating in flight and reproductive activities and identify the most representative population reproduction and migration models for *M. separata* as well as provide a theoretical framework for determining the dynamics of populations to predict insect occurrence trends to prevent outbreaks of this pest.

Materials and methods

Insects

The *M. separata* samples in this experiment originated from field-collected individuals from Zhangjiakou, Hebei Province (41.85°N, 114.60°E); the population had been maintained for three generations in the laboratory at 23 ± 1 °C, 70% relative humidity (RH) and a photoperiod of 14:10 (light: dark). Larvae were reared with fresh corn seedlings as a food source in round glass bottles (9 cm × 13 cm, diameter × height) for pupation (10 larvae per bottle). After emergence, singe female and male were paired and transferred to cylindrical plastic cages (10 cm × 20 cm, diameter × height) for oviposition, and they were supplied with a 10% honey solution (vol:vol) until death.

Tethered flight

Flight tests of all treated moths (one male and one female unique pairs) at the same age were conducted in a flight mill system that automatically recorded the flight data (flight duration, flight distance and average flight velocity), as mentioned in Qin *et al.* (2018). Before the flight tests, all age-paired moths (initiated with 1-day-old adults) were tethered using a technique outlined in previous work (Jiang *et al.*, 2010; Cheng *et al.*, 2012) and fed a honey solution.

Flight frequency treatments

To detect the effects of flying males on ovarian and reproductive development and the flight capacity of females according to their flight frequency, the males were divided into a flying group (males and females both flew) and a nonflying male group (only the females flew). All the treatments were initiated with 1-day-old adults and paired (one male and one female) by the same age. Flight durations of 0, 1, 2, 3, 4 and 5 nights were established under laboratory: the nonflying moths (0 flights) served as controls, moths that flew on the day 1 after emergence (one flight), days 1–2 (two flights), days 1–3 (three flights), days 1–4 (four flights), and days 1–5 (five flights), with a tethered flight for 12 h from 20:00 to 08:00, a period optimal for studying *M. separata* flight behaviour (Luo *et al.*, 1999; Lv *et al.*, 2014; Zhang *et al.*, 2020). Then, the effects of flying males on reproduction and flight frequency of adults were estimated by comparing the two male groups. To ensure the accuracy of the experimental results, all tether tests were conducted under dark conditions, and all the treatment moths were attached a short tether for 5 days. More than 25 pairs in each treatment were dissected for this experiment.

Reproductive parameters, ovarian development levels and flight capacity

After completion of the tethered flight, all treated females were paired with males of the same age (one male and one female) and placed in cylindrical plastic cages with fresh honey solution as a food source under the same laboratory conditions as before: 23 ± 1 °C, 70% RH, and a photoperiod of 14:10 (light: dark). Reproductive parameters including lifetime fecundity, preoviposition period (POP), period of first oviposition (PFO), oviposition period, female and male longevity, mating frequency and mating rate were recorded using the method of Zhang *et al.* (2015, 2020).The POP was used to calculate the duration between adult emergence and the first oviposition. The PFO was a major parameter to evaluate the synchronization of first laying-eggs, describing the time window from female's POP to the minimal POP.

The ovarian development grades and mating rates were determined after female death. The calculation of the ovarian development level followed the standard protocol, which has been described elsewhere. The ovarian development levels were divided into five grades according to the maturity of the ovary (Chen *et al.*, 2019). The flight capacity (flight duration, flight distance and average flight velocity) of adults was calculated from the data recorded by the flight mill system. The ovarian development levels were divided into five grades as described

Data analysis

Prior to analysis, all data from this experiment were checked for homogeneity of variance. All reproductive parameters and flight capacities were analysed by a two-way analysis of variance (ANOVA) with flight frequency (six levels) and males (flew and not flew) as factors using Tukey's test (HSD) for mean comparisons. Pearson's correlation analysis was applied to examine the influences of flight capacity and flight frequency of males on

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reproductive development of age-paired females. All statistical analyses were carried out using SAS 9.20 software (SAS Institute, Cary, NC).

Results

Reproductive performances of M. separata *adults treated with different flight frequency*

POP was significantly affected by the flight frequency and the interaction between flight frequency and male groups, while the male groups had no effect on the POP (tables 1 and 2). Compared to that of the male-nonflying group, the POP of females in the male-flying group was significantly shortened in the one ($F_{1,\ 58} = 7.76$, $P = 0.007$) and two night groups ($F_{1,\ 58} = 4.47$, $P = 0.039$); however, it was significantly prolonged when the moths flew for three nights ($F_{1,\ 56} = 7.42$, $P = 0.009$, table 2). There were significant differences in POP of females treated by different flight frequency (male-flying group: $F_{5,\ 164} = 28.75$, $P < 0.001$; male-nonflying group: $F_{5,\ 164} = 10.88$, $P < 0.001$). In the male-flying group, the POP of adults that flew for one and two nights was significantly shorter than the controls (0 nights), resulting in these females beginning to lay eggs significantly earlier than the controls; on the contrary, the POP was significantly increased in adults that flew for more than two nights, which showed a significant delay in reproductive development compared to the controls, one and two nights (table 2). In the male-nonflying group, the POP of females that flew for one and two nights was also significantly shorter than the controls; however, it was significantly prolonged in adults that flew for five nights (table 2).

Flight frequency and male groups had significant influences on the lifetime fecundity but there was no significant interaction (tables 1 and 2). Lifetime fecundity was significantly decreased with the increasing flight frequency (male-flying group: $F_{5,\ 164} = 22.91$, $P < 0.001$; male-nonflying group: $F_{5,\ 164} = 10.19$, $P < 0.001$), and it was significantly reduced in the three-, four- and five-night flight treatments compared to the controls, one- and two-nights in the male-flying group. Interesting, in the male-nonflying group, the moths in the four- and five-night flight treatments also produced fewer eggs than the females from the one- and two-night flight treatments (tables 1 and 2). Compared to the lifetime fecundity in the male-nonflying group at the same flight frequency, the lifetime fecundity in the male-flying group was significantly reduced in the four-night flight group ($F_{1,\ 52} = 3.99$, $P = 0.050$, table 2).

The oviposition period was significantly affected by the flight frequency, male groups and their interaction (tables 1 and 2). Compared to the male-nonflying group, the oviposition period in the flying male-group was significantly increased in the one-, two- and four-night flight groups (one night: $F_{1,\ 58} = 4.23$, $P = 0.044$, table 2; two nights: $F_{1,\ 56} = 9.90$, $P = 0.003$; four nights: $F_{1,\ 52} = 5.20$, $P = 0.027$). Flight frequency significantly affected the oviposition periods of moths (male-flying group: $F_{5,\ 164} = 4.84$, $P < 0.001$; male-nonflying group: $F_{5,\ 164} = 8.18$, $P < 0.001$). The one- and two-night flight treatments significantly increased the oviposition period compared to the five-night flight treatments in the male-flying group. However, the oviposition period of moths at each frequency was significantly less than the controls in the male-nonflying group (table 2).

Flight frequency significantly affected the PFO, mating frequency and mating rate (tables 1 and 2). The PFO of moths in the male-flying group was significantly reduced in the one-night group ($F_{1,\ 58} = 5.00$, $P = 0.029$) and two-night group ($F_{1,\ 58} = 4.47$, $P = 0.039$) compared to the male-nonflying group. There were significant differences in the PFO of moths that in the 0–5 flight nights groups between the two male groups (male-flying group: $F_{5,\ 164} = 4.77$, $P < 0.001$; male-nonflying group: $F_{5,\ 164} = 2.77$, $P = 0.020$). In the male-flying group, the PFO of adults that flew for two nights was significantly less than that of moths from the controls and flew for five nights. Likely, the oviposition time of females that flew for two nights was significantly more synchronous than those in the controls, four- and five-nights in the male-nonflying group, with PFO was significantly less 1.05 days and 1.38 days, respectively (table 2). Although no significant differences were observed in the mating frequency and mating rate between the two male groups at the same flight frequency, there were significant differences among the different flight frequency groups. In the male-flying group, the mating frequency ($F_{5,\ 164} = 5.53$, $P < 0.001$) and mating rate ($F_{5,\ 164} = 3.79$, $P = 0.003$) of adults that flew for four and five nights were significantly lower than those in the one and 1–2 night flight treatments.

The female longevity was also significantly affected by the flight frequency and male groups but not by their interaction (tables 1 and 2). The longevity of females that flew for 1–3 nights was significantly higher in the male-flying group than that in the male-nonflying group (one night: $F_{1,\ 58} = 5.22$, $P = 0.026$; two nights: $F_{1,\ 56} = 8.21$, $P = 0.006$; three nights: $F_{1,\ 56} = 12.23$, $P = 0.001$, table 2). Flight frequency and the interaction between flight frequency and male groups had significant effects on the male longevity (tables 1 and 2). The longevity of males that flew for one and two nights was significantly higher than that of the non-flying males (one night: $F_{1,\ 58} = 4.76$, $P = 0.033$; two nights: $F_{1,\ 56} = 6.20$, $P = 0.016$), while it was significantly decreased in the five-nights group ($F_{1,\ 48} = 6.57$, $P = 0.003$). In the male-flying group, the male longevity in moths that flew for one and two nights significantly exceeded that of those that flew for four and five nights ($F_{5,\ 164} = 8.61$, $P < 0.001$). No significant differences were found in the nonflying group ($F_{5,\ 164} = 1.08$, $P = 0.375$, table 2).

Ovarian development of M. separata *adults treated with different flight frequency*

Ovarian development was significantly affected by the flight frequency, male treatment and their interaction (tables 1 and 2). Comparisons of ovarian development between the two flying male groups at each flight frequency showed that ovarian development was significantly slower in the male-flying group than that in the male-nonflying group in moths that flew for three and four nights (three nights: $F_{1,\ 56} = 12.39$, $P = 0.001$; four nights: $F_{1,\ 52} = 4.63$, $P = 0.036$). The ovarian development grade in females that flew for one and two nights was significantly higher than that in the controls and the other flight frequency groups in the male-flying group ($F_{5,\ 164} = 21.97$, $P < 0.001$). Likewise, the ovarian development grade of females was also significantly increased in the one- and two-night flight treatments compared to the controls, four- and five-night flight treatments in the male-nonflying group ($F_{5,\ 164} = 8.58$, $P < 0.001$, table 2).

Comparison of female flight capacity between the two male groups

The flight duration and flight distance were significantly affected by male groups, flight frequency and the interaction between

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Table 1. Results of two-way ANOVA analysis on effects of flight frequency and male groups (flying or nonflying males) on female reproductive parameters for *M. separata*

Parameters	Source	df	MS	*F*	*P*
POP (d)	Male groups	1	0.005	0.004	0.952
	Flight frequency	5	52.785	36.890	<0.001
	Male groups × Flight frequency	5	3.911	2.733	0.020
	Error	326	1.431		
Lifetime fecundity	Male groups	1	362,591.406	4.367	0.037
	Flight frequency	5	2,480,334.586	29.875	<0.001
	Male groups × Flight frequency	5	117,234.843	1.412	0.219
	Error	326	83,024.800		
Oviposition period (d)	Male groups	1	37.996	10.084	0.002
	Flight frequency	5	34.517	9.160	<0.001
	Male groups × Flight frequency	5	9.464	2.511	0.030
	Error	326	3.768		
PFO (d)	Male groups	1	0.829	0.610	0.435
	Flight frequency	5	9.638	7.092	<0.001
	Male groups × Flight frequency	5	1.252	0.922	0.467
	Error	326	1.359		
Mating frequency	Male groups	1	0.430	1.449	0.230
	Flight frequency	5	1.945	6.551	<0.001
	Male groups × Flight frequency	5	0.395	1.331	0.250
	Error	326	0.297		
Mating percentage	Male groups	1	0.022	0.091	0.763
	Flight frequency	5	0.962	4.029	0.001
	Male groups × Flight frequency	5	0.183	0.766	0.575
	Error	326	0.239		
Female longevity (d)	Male groups	1	56.766	12.448	<0.001
	Flight frequency	5	16.302	3.575	0.004
	Male groups × Flight frequency	5	9.804	2.150	0.059
	Error	326	4.560		
Male longevity (d)	Male groups	1	6.877	0.437	0.509
	Flight frequency	5	77.531	4.930	<0.001
	Male groups × Flight frequency	5	58.921	3.746	0.003
	Error	326	15.727		
Ovarian development grade	Male groups	1	0.740	4.457	0.036
	Flight frequency	5	4.018	24.211	<0.001
	Male groups × Flight frequency	5	0.377	2.272	0.047
	Error	326	0.166		

flight frequency and male treatment (tables 3 and 4). Although all flight parameters in the male-flying group were less than those in the male-nonflying group, the flight duration was significantly lower in only those that flew for four nights ($F_{1,\ 52} = 8.71$, $P = 0.005$) and five nights ($F_{1,\ 48} = 9.34$, $P = 0.004$). In addition, flight duration was prolonged with increasing flight frequency, which was significantly decreased in moths that flew for 1–2 night compared to those that flew for four and five nights in the male-flying group ($F_{4,\ 135} = 16.91$, $P < 0.001$) and male-nonflying group ($F_{4,\ 135} = 40.51$, $P < 0.001$), respectively (table 4).

Compared to those in the male-nonflying group, the flight distances of females that flow for three, four and five nights were significantly decreased in the male-flying group (three nights: $F_{1,\ 56} = 5.51$, $P = 0.023$; four nights: $F_{1,\ 52} = 8.84$, $P = 0.004$; five nights: $F_{1,\ 48} = 10.18$, $P = 0.003$). Similar results were obtained for the flight distance with flight frequency in the male-flying group

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Table 2. Reproductive performances of *M. separata* adults between the two male groups treated by different flight frequency

		Flight frequency					
Parameters	Male treatments	0	1	2	3	4	5
POP (d)	Flying	5.39 ± 0.24 b A	4.00 ± 0.16 c B	4.52 ± 0.13 c B	6.28 ± 0.20 a A	6.33 ± 0.25 a A	6.96 ± 0.29 a A
	Nonflying	5.77 ± 0.35 b A	4.63 ± 0.16 c A	4.93 ± 0.15 c A	5.45 ± 0.23 bc B	6.07 ± 0.21 ab A	6.88 ± 0.26 a A
Lifetime fecundity (eggs per female)	Flying	760.96 ± 68.56 a A	852.40 ± 45.49 a A	798.79 ± 45.40 a A	522.48 ± 42.48 b A	398.67 ± 47.30 bc B	254.20 ± 42.95 c A
	Nonflying	683.33 ± 54.45 ab A	902.60 ± 58.92 a A	806.62 ± 53.42 a A	679.72 ± 71.42 ab A	564.85 ± 56.96 bc A	363.04 ± 51.27 c A
Oviposition period (d)	Flying	5.37 ± 0.40 ab A	5.87 ± 0.31 a A	6.28 ± 0.39 a A	4.97 ± 0.30 ab A	5.33 ± 0.35ab A	3.84 ± 0.46 b A
	Nonflying	6.47 ± 0.45 a A	4.97 ± 0.31 b B	4.72 ± 0.31 bc B	4.21 ± 0.39 bc A	4.19 ± 0.36 bc B	3.36 ± 0.35 c A
PFO (d)	Flying	1.39 ± 0.24 ab A	1.00 ± 0.16 bc B	0.52 ± 0.13 c B	1.28 ± 0.20 abc A	1.33 ± 0.25 abc A	1.96 ± 0.29 a A
	Nonflying	1.77 ± 0.35 a A	1.50 ± 0.16 ab A	0.93 ± 0.15 b A	1.31 ± 0.19 ab A	1.93 ± 0.19 a A	1.84 ± 0.25 a A
Mating frequency	Flying	0.75 ± 0.13 ab A	0.87 ± 0.08 a A	0.93 ± 0.12 a A	0.69 ± 0.11 abc A	0.41 ± 0.10 bc A	0.28 ± 0.09 c A
	Nonflying	0.63 ± 0.10 a A	0.80 ± 0.10 a A	0.66 ± 0.09 a A	0.48 ± 0.09 a A	0.44 ± 0.10 a A	0.48 ± 0.10 a A
Mating rate (%)	Flying	60.71 ± 9.40 ab A	80.00 ± 7.43 a A	65.52 ± 8.98 a A	55.17 ± 9.40 ab A	40.74 ± 9.64 b A	28.00 ± 9.17 b A
	Nonflying	60.00 ± 9.10 a A	66.67 ± 8.75 a A	58.62 ± 9.31 a A	48.27 ± 9.44 a A	44.44 ± 9.75 a A	48.00 ± 10.20 a A
Female longevity (d)	Flying	11.23 ± 0.58 a A	10.53 ± 0.36 a A	10.52 ± 0.43 a A	10.86 ± 0.30 a A	10.74 ± 0.39 a A	10.16 ± 0.40 a A
	Nonflying	11.40 ± 0.38 a A	9.27 ± 0.42 b B	8.97 ± 0.32 b B	9.17 ± 0.38 b B	9.80 ± 042 ab A	10.08 ± 0.29 ab A
Male longevity (d)	Flying	14.10 ± 0.86 ab A	16.37 ± 0.99 a A	16.41 ± 0.83 a A	13.83 ± 0.85 ab A	12.15 ± 0.70 b A	11.20 ± 0.82 b B
	Nonflying	13.93 ± 0.83 a A	13.87 ± 0.57 a B	13.90 ± 0.58 a B	14.03 ± 0.53 a A	12.44 ± 0.51 a A	14.28 ± 0.56 a A
Ovarian development grade	Flying	4.27 ± 0.08 b A	4.73 ± 0.08 a A	4.62 ± 0.09 a A	4.14 ± 0.07 b B	4.07 ± 0.05 b B	4.04 ± 0.04 b A
	Nonflying	4.23 ± 0.08 b A	4.67 ± 0.09 a A	4.66 ± 0.09 a A	4.38 ± 0.09 ab A	4.30 ± 0.09 b A	4.00 ± 0.00 b A

Data in the table are mean ± SE. Different lowercase letters in the same row represent significant differences between different flight frequency by Tukey's HSD test at 5% level. Means in the same column followed by the same uppercase letter do not differ significantly ($P < 0.05$) by Tukey's HSD test.

Table 3. Results of two-way ANOVA analysis on effects of flight frequency and male groups (flying or nonflying males) on female flight parameters.

Parameters	Source	df	MS	*F*	*P*
Flight duration (h)	Male groups	1	630.709	25.599	<0.001
	Flight frequency	4	1381.841	56.085	<0.001
	Male groups × Flight frequency	4	67.030	2.721	0.030
	Error	270	24.638		
Flight distance (km)	Male groups	1	10,422.607	30.850	<0.001
	Flight frequency	4	16,245.956	48.086	<0.001
	Male groups × Flight frequency	4	1306.518	3.867	0.005
	Error	270	337.852		
Average velocity (km h^{-1})	Male groups	1	14.668	17.430	<0.001
	Flight frequency	4	4.486	5.331	<0.001
	Male groups × Flight frequency	4	1.500	1.782	0.133
	Error	270	0.842		

Table 4. Flight capacity of *M. separata* females between the two male groups treated by different flight frequency

		Flight frequency				
Parameters	Male treatments	1	2	3	4	5
Flight duration (h)	Flying	2.67 ± 0.44 d A	4.79 ± 0.68 cd A	6.82 ± 1.12 bc A	9.75 ± 1.04 ab B	12.61 ± 1.23 a B
	Nonflying	3.27 ± 0.44 cd A	6.58 ± 0.70 cd A	8.80 ± 0.74 c A	14.54 ± 1.24 b A	18.50 ± 1.48 a A
Flight distance (km)	Flying	6.76 ± 1.24 d A	11.83 ± 2.03 cd A	16.63 ± 3.12 bc B	25.57 ± 3.38 b B	38.46 ± 5.06 a B
	Nonflying	10.56 ± 2.12 d A	15.82 ± 2.09 cd A	25.25 ± 2.66 c A	41.95 ± 4.35 b A	65.83 ± 6.92 a A
Flight velocity (km h^{-1})	Flying	2.33 ± 0.14 ab B	2.36 ± 0.18 ab A	2.20 ± 0.13 b B	2.62 ± 0.14 ab A	2.87 ± 0.18 a B
	Nonflying	2.90 ± 0.23 ab A	2.41 ± 0.18 b A	3.05 ± 0.20 ab A	2.81 ± 0.15 ab A	3.49 ± 0.18 a A

Data in the table are mean ± SE. Different lowercase letters in the same row represent significant differences between different flight frequency by Tukey's HSD test at 5% level. The same uppercase letter in a same column indicates no significant difference between the two male groups by Tukey's HSD test at 5% level.

($F_{4,\ 135} = 15.57$, $P < 0.001$) and male-nonflying group ($F_{4,\ 135} = 32.64$, $P < 0.001$, table 4). Male groups and flight frequency had significant effects on the mean velocity; however, their interaction had no influence (tables 3 and 4). The average velocities of moths that flew for one, three and five nights in the male-flying group were significantly slower than those in the male-nonflying group (one night: $F_{1,\ 58} = 4.52$, $P = 0.038$; three nights: $F_{1,\ 56} = 12.75$, $P = 0.001$; five nights: $F_{1,\ 48} = 6.15$, $P = 0.017$). Moths that flew for three nights had the lowest average velocity, with a velocity of less than 0.67 km h^{-1}, compared to the highest those that flew for five nights in the male-flying group ($F_{4,\ 135} = 3.32$, $P < 0.013$), while the lowest mean velocity of moths that flew for two nights was observed in the male-nonflying group ($F_{4,\ 135} = 3.99$, $P = 0.004$, table 4).

Correlation of flight capacity of males, with reproduction of age-paired females

The correlation analysis (table 5) suggested a positive correlation between flight frequency and flight duration and distance of males with POP and PFO of age-paired females, but the relationship with the lifetime fecundity, oviposition period, mating frequency, ovarian development grade of age-paired females showed a significantly negative correlation. Collectively, these results suggested that flight capacity of males was negatively correlated with reproduction of age-paired females with the increase of flight frequency.

Discussion

Comparisons of *M. separata* reproductive performance and degree of ovarian development between the two male treatment groups at the same frequency revealed that males played a crucial role in reproductive and migratory regulation. Females that flew for 1–2 nights in the flying male group had a significantly shorter POP and PFO than those in the nonflying group, and the oviposition period and longevity of the females were significantly increased. In contrast, flight for more than two nights induced prolonged POP and PFO, as well as decreased lifetime fecundity, a decreased mating frequency, a decreased mating rate and a lower degree of ovarian development. In the current study, reproductive variations in response to different flight treatments were evaluated by assessing the POP, PFO and other reproductive parameters in a migratory insect (Jiang *et al.*, 2010; Cheng *et al.*, 2012). A decrease in lifetime fecundity and an increase in POP are generally considered major reproductive costs of migration (Gunn *et al.*, 1989;

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Table 5. Pearson's correlations of flight distance (km), flight velocity (km h^{-1}), and flight duration (h) of males, with reproductive parameters of age-paired females

	Flight frequency		Flight duration		Flight distance		Flight velocity	
Parameters	*r*	*P*-value	*r*	*P*-value	*r*	*P*-value	*r*	*P*-value
POP	0.442	<0.001	0.383	<0.001	0.353	<0.001	0.096	0.214
PFO	0.098	0.037	0.187	0.015	0.162	0.036	−0.047	0.545
Lifetime fecundity	−0.577	<0.001	−0.419	<0.001	−0.415	<0.001	−0.248	0.001
Oviposition period	−0.246	0.001	−0.179	0.020	−0.206	0.007	−0.078	0.316
Mating frequency	−0.301	<0.001	−0.224	0.003	−0.199	0.010	−0.090	0.249
Mating rate	−0.260	0.001	−0.193	0.012	−0.136	0.080	−0.039	0.613
Female longevity	−0.096	0.213	−0.055	0.481	−0.096	0.216	−0.094	0.226
Male longevity	−0.286	<0.001	−0.222	0.004	−0.276	<0.001	−0.111	0.153
Ovarian development grade	−0.406	<0.001	−0.273	<0.001	−0.288	<0.001	−0.162	0.036

Gibbs and Dyck, 2010). Overall, the results showed that flying males significantly promoted ovarian and reproductive development in *M. separata* that flew continuously for 1–2 nights compared to nonflying males; however, they could have the opposite effect for other flight frequencies.

To our knowledge, *M. separata* spends several nights flying long distances to reach breeding areas (Chen *et al.*, 1989). However, when *M. separata* migration begins and whether the first migratory period is consistent in males and females is still unknown. Prior studies found that some insects, such as *Mythimna separata* (Lin, 1990), initiated their migration soon after eclosion when the ovaries of females were still immature (stage I or II). Luo *et al.* (1999) reported that in *M. separata* adults, flight at only 1 day after emergence significantly stimulated reproduction in different flight-age tests. Zhang *et al.* (2008) further observed that the first 24 h after emergence was a crucial time window for switching migrants into residents in *M. separata*. In addition, our previous study demonstrated that a positive effect of migration on reproduction occurred in only newly emerged (24 h) females that flew within 12 h (Lv *et al.*, 2014). Therefore, it is supposed that the 1st day after emergence may be the primary migratory time period for *M. separata* (Jiang *et al.*, 2014*b*). Similarly, recent research on *Cnaphalocrocis medinalis* proved that the first migration most likely occurred within the first 2 days after eclosion (Zhang *et al.*, 2015).

The results of the flight frequency tests in the two male treatment groups showed that females in the male-flying male group that flew for 1–2 nights achieved faster ovarian and reproductive development because their POP was significantly shortened and their degree of ovarian development was significantly increased compared to those in the control group. In addition, their lifetime fecundity, mating frequency and mating rate were higher than those in the controls; their PFO was lower than that in the controls, and a significant decrease was found in adults that flew for two nights. By contrast, more than three nights of flight significantly inhibited reproductive and ovarian development, and the negative influence significantly intensified as flight frequency increased. Pearson's correlation analysis had also demonstrated that flight capacity of males had significantly negative correlations with reproduction of age-paired females with increasing the flight frequency.

In the male-nonflying group, the POP of adult females that flew for 1–2 nights was also significantly reduced compared to those in the controls. Furthermore, significant decreases in lifetime fecundity, mating frequency and the mating rate were observed in those that flew for 4–5 nights. Adults that flew for more than three nights had significantly decreased reproductive development compared to the controls and those that flew for one or two nights, suggesting that in females, migration for three nights resulted in significant reproductive costs. Hence, we supposed that males that flew for 1–2 nights significantly stimulated ovarian and reproductive development in females and weakened the flight willingness of females, with a decrease in flight frequency from 3 to 2. Insect migration occurs when the benefits of flight exceed the reproductive costs of migration (Chapman *et al.*, 2012). Based on these results, we also hypothesized that *M. separata* individuals began their first migration within 2 days after eclosion and completed their migratory flight within two nights; otherwise, they would pay substantial reproductive costs. This speculation had been supported by radar observations (Chen *et al.*, 1995).

One possible reason might be their flight ability. Analysis of the flight capacity between the two male treatment groups revealed that the flight capacity of females in the flying male group was significantly weaker than that of females in the nonflying group because their flight duration and flight distance decreased with increasing flight frequency; significant decreases were observed in moths that flew for more than two nights and more than three nights, respectively. It is well known that a trade-off between migration and reproduction exists (Lorenz, 2007). Limited internal resources are invested more in reproduction, thereby reducing the energy supply for flight, resulting in a decrease in flight capacity. Migratory and mating behaviours of *M. separata* occurred during the POP (Luo *et al.*, 1999; Zhao *et al.*, 2009; Jiang *et al.*, 2011). Interestingly, the number of female *M. separata* was significantly higher than that of males during the first migratory stage (1–4 day after emergence) in light trapping experiments (Li *et al.*, 1987; Lin, 1990; Zhang *et al.*, 2018). It was also reported that the proportion of captured females gradually decreased following the age delay due to the maturation of the ovaries and impaired flight capacity in female *M. separata* (Wang and Zhang, 2001). Thus, we deduced that flying males significantly stimulated ovarian and reproductive development in females that flew for 1–2 nights at the expense of reducing subsequent flight capacity. Flying males impaired the flight capacity of age-paired females, which was conducive to reduce

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inconsistencies in the time of first migration between females and males and increase mating frequencies, thereby promoting ovarian development and reproductive development of *M. separata*. Our results are consistent with the previous findings that females emerging when and where male density is high tend to have a higher mating success, which results in increasing the proportion of mated females with mature oocytes among migrants (Gerber and Walkof, 1992; Coombs *et al*., 1993; Rhainds, 2010).

Another possible reason is related to JH, which regulates many essential physiological processes in insects, such as ovarian and flight muscle development (Luo *et al*., 2001; Moon and Kim, 2003; Saha *et al*., 2016). Cusson *et al*. (1990) found that *Pseudaletia unipuncta* adults were transferred from 15 to 25 °C resulted in a marked increase in JH biosynthesis within 24 h. Heinrich (1993) reported that there was a significant increase in body temperature caused by active flight. Thus, the occurrence of sexual maturation and mating success within several days of initiating migratory flight is not a total surprise based on the above points (Zhao *et al*., 2009). Migratory flight may increase fecundity under certain conditions (Rankin *et al*., 1986; Luo *et al*., 1999). High JH levels are strongly associated with the rapid development of the ovaries, accelerating the degradation of flight muscles, resulting in the inhibition of migratory ability (Zera, 2007; Sun *et al*., 2013). This onset of maturation is beneficial to mate and initiate oviposition as soon as possible after relocate suitable breeding habitats for migrant females (Wada *et al*., 1988).

In summary, our laboratory study demonstrated that *M. separata* individuals began their first migration within 2 days after eclosion and flew for two nights. The first migration period of females and males was not identical; female initiated their migration earlier than males due to a stronger flight capacity. Flying males significantly stimulated ovarian and reproductive development in females that flew for two nights, resulting in a subsequently weakened flight capacity and decreased flight propensity in females. These findings provide valuable information regarding the complex process of migration in *M. separata*. In the future, additional laboratory studies combined with field tests will be carried out to elucidate the mechanism of migration and outbreaks for the development of pest prevention and control strategies.

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