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Abstract

The beet armyworm, *Spodoptera exigua*, undertakes long-distance migration. We used flight mills to investigate the interaction between flight and reproduction in this species given the apparent absence of the oogenesis-flight syndrome. This syndrome, common in many migratory insects, is characterized by a suite of traits including migration during the pre-oviposition period followed by a switch to oogenesis. No negative effects of inter-ovipositional flight on lifetime fecundity were observed. Instead, adult reproductive output suffered when female flight was initiated the first day after eclosion and before oviposition, suggesting that migratory flight overlaps with the oviposition period rather than being confined to the pre-oviposition period. Mating status of both females and males had no negative influence on their flight performance except that flight distance and flight duration of 7-day-old mated females were significantly less than in unmated females. Furthermore, the number of eggs produced and mating frequency of females less than 7 days of age were not significantly correlated with flight performance, suggesting reproductive development paralleled and was independent of migratory behavior. This independent relationship between flight and reproduction of adults is consistent with the very short pre-oviposition period in this species, and suggests that resources are partitioned between these activities during pupal development. Together, our results uncovered neither obvious trade-offs nor mutual suppression between flight and reproduction in *S. exigua*, which indicates the lack of an oogenesis-flight syndrome for coordination of these two energy-intensive processes. We propose a conceptual model of migration for this species based on the current and previous studies.

Keywords

Spodoptera exigua, Oogenesis-flight syndrome, Flight Reproduction, Migration

Disciplines

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Comments

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Relationship of flight and reproduction in beet armyworm, *Spodoptera exigua* (Lepidoptera: Noctuidae), a migrant lacking the oogenesis-flight syndrome

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ABSTRACT

The beet armyworm, *Spodoptera exigua*, undertakes long-distance migration. We used flight mills to investigate the interaction between flight and reproduction in this species given the apparent absence of the oogenesis-flight syndrome. This syndrome, common in many migratory insects, is characterized by a suite of traits including migration during the pre-oviposition period followed by a switch to oogenesis. No negative effects of inter-ovipositional flight on lifetime fecundity were observed. Instead, adult reproductive output suffered when female flight was initiated the first day after eclosion and before oviposition, suggesting that migratory flight overlaps with the oviposition period rather than being confined to the pre-oviposition period. Mating status of both females and males had no negative influence on their flight performance except that flight distance and flight duration of 7-day-old mated females were significantly less than in unmated females. Furthermore, the number of eggs produced and mating frequency of females less than 7 days of age were not significantly correlated with flight performance, suggesting reproductive development paralleled and was independent of migratory behavior. This independent relationship between flight and reproduction of adults is consistent with the very short pre-oviposition period in this species, and suggests that resources are partitioned between these activities during pupal development. Together, our results uncovered neither obvious trade-offs nor mutual suppression between flight and reproduction in *S. exigua*, which indicates the lack of an oogenesis-flight syndrome for coordination of these two energy-intensive processes. We propose a conceptual model of migration for this species based on the current and previous studies.

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1. Introduction

Insect migration, as a component of life history, plays an important role in population maintenance and evolution. It is presumed to be a costly behavior, with adult reproduction suffering a trade-off in energy needed for adult flight apparatus construction and flight fuel versus ovarian development, or oogenesis (Rankin and Burchsted, 1992; Crowley and McLetchie, 2002; Ronce, 2007). The cost is usually manifested, especially in wing dimorphic species, as decreased reproductive output caused by a prolonged pre-oviposition period, decreased longevity, and decreased lifetime egg production (Dingle and Arora, 1973; Walters and Dixon, 1983; Roff, 1984; Zera, 1984; Zera and Mole, 1994). Physiological management of the migration–reproduction trade-off often includes a package of adaptations referred to as the oogenesis-flight syndrome, which was taken for many years as a

fundamental trait of insect migrants (Johnson, 1969; Rankin et al., 1986, 1994; Colvin and Gatehouse, 1993; Keil et al., 2001; Gu et al., 2006; Lorenz, 2007). The syndrome describes a pattern in which the flight apparatus develops soon after eclosion to support migratory flight, migratory flight is initiated during the adult pre-reproductive stage when ovarian development and mating behavior are suppressed, and females switch to egg development and oviposition activity rapidly after termination of migration.

However, the nature of trade-offs between reproduction and migration, and of the relationship between the physiological processes underpinning these life history traits is not simple, with the consequence that the oogenesis-flight syndrome is not a universal characteristic of migratory insects (Rankin et al., 1986; Sappington and Showers, 1992; Jervis et al., 2005; Zhao et al., 2009). Examples of wing monomorphic species that engage in both migratory flight and reproductive development simultaneously are not uncommon (Johnson, 1969; Greenbank et al., 1980; Sappington and Showers, 1992; McNeil et al., 1995; Russell et al., 1998; Isaacs and Byrne, 1998; Asplen et al., 2009; Zhao et al., 2009), demonstrating that the two processes, while fundamentally antagonistic in the sense that they draw on the same limited pool

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of internal resources (Wheeler, 1996), are not fundamentally antagonistic in terms of developmental timing.

The beet armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae), has become a serious economic pest of vegetables and cotton in recent years across a wide distribution in China (Jiang and Luo, 1998a, 1999; Wang et al., 2002, 2007; Wu et al., 2008). Like many noctuid pests, it is a long-distance migratory species (Mikkola, 1970; Yathom, 1971; Oku and Kobayashi, 1978; Mitchell, 1979; Kimura, 1991; Adamczyk et al., 2003; Feng et al., 2003), with one of the greatest documented expanses traversed by any migratory noctuid of 3500 km (Mikkola, 1970). In China, this species cannot overwinter north of about 38°N where the isotherm in January is about -4°C (Jiang et al., 2001). Thus, annual infestations of Northeast and Northwest China (Jiang and Luo, 1998a, 1999; Luo et al., 2000) must be comprised of immigrants from southern China, an inference supported by radar observations (Feng et al., 2003) and molecular genetic markers (Niu et al., 2006).

Tethered flight tests on flight mills in the laboratory also indicate strong migratory capacity, with longest flight distance and flight duration reaching 179 km and 50 h, respectively (Jiang and Luo, 1998b). Flight behavior is influenced by several environmental and physiological factors (Jiang and Luo, 1998b; Jiang et al., 1999, 2000, 2002). Both males and females can mate on the first night after emergence, with first mating on the first or second night being optimal in terms of lifetime fecundity, and there is a short pre-oviposition period of approximately 2 days (Chu and Wu, 1992; Rogers and Marti, 1996, 1997; Jiang, 1999; Tisdale and Sappington, 2001) that is not influenced by environmental factors (Jiang et al., 1999, 2000, 2002). This raises important questions about *S. exigua*'s movement ecology: (i) Given that most long-distance migratory insects exhibit the oogenesis-flight syndrome, i.e. migrate before reproductive maturation (Kennedy, 1961; Johnson, 1969; Luo et al., 1999), and that the beet armyworm likewise initiates migratory flight before oviposition, how can such a short pre-oviposition period allow successful completion of long-distance migration? (ii) What is the effect of migration during the oviposition period on reproduction? Is there a reproductive cost to migration (Rankin and Burchsted, 1992; Dingle and Arora, 1973; Walters and Dixon, 1983; Roff, 1984; Zera, 1984; Zera and Mole, 1994)? (iii) Do adults have enough flight potential after mating and oviposition to support successful long-distance migration? Does copulation and oviposition influence flight performance, and what is the biological and evolutionary significance of migrating during the oviposition period?

Aspects of the relationship between overwintering, migration and reproduction in *S. exigua* in China were examined by Jiang (1999), providing a solid basis for understanding its migratory life history strategy. Furthermore, the influences of moth age, female mating status and ovarian development on flight capacity have been elucidated by Jiang and Luo (1998b) and Han et al. (2008). Based on age-related flight behavior and reproductive development (Jiang and Luo, 1998b; Jiang, 1999), we deduced that this species does not exhibit the oogenesis-flight syndrome. This conclusion was confirmed directly with flight mill studies by Han et al. (2008). Several factors affect realized lifetime fecundity of *S. exigua*, including larval and adult diet, pupal size, and age of first mating (Rogers and Marti, 1996, 1997; Greenberg et al., 2001; Tisdale and Sappington, 2001). However, the influence of flight on reproductive output, often seen as a reproductive cost of migration, and the interaction of mating frequency and oviposition on flight remain unknown.

In this study, we designed two synergistic experiments to examine the reciprocal influences of flight and reproduction on one another, which can provide further insight into the relationship between these two energetically expensive processes in the absence of the oogenesis-flight syndrome. In addition, we put forward a conceptual migratory model for this species incorporat-

ing the accumulated insights gathered over the last several years. These results provide helpful information toward establishing effective population monitoring and forecasting projects for *S. exigua*, as well as expanding our awareness of the variety of migration strategies employed by insects.

2. Materials and methods

2.1. Insects

S. exigua used in the experiments were from a colony that originated from a population collected near Beijing, China (115.58°E, 40.18°N). The colony had been maintained for four generations when the experiments began. Larvae were reared on artificial diet as described previously (Jiang et al., 1999) at a constant temperature of $28 \pm 1^{\circ}\text{C}$, 60–70% RH and photoperiod of 14L:10D (light period was from 07:00 to 21:00). Pupae were sexed on the third day and adult males and females were allowed to emerge in separate transparent containers. Except for special requirements of experimental treatments, adults were transferred in pairs to 850-mL jars provided with wax paper for oviposition. Jars were covered with gauze to facilitate ventilation and adults were provided with 5% honey solution (v/v).

2.2. Experimental design

Two reciprocal experiments were designed in this study. The first was conducted to detect the influence of flight by moths of different ages on reproductive traits, including pre-oviposition period, oviposition period, fecundity, mating frequency and moth longevity. Approximately 170 male–female pairs were placed in separate 850-mL jars set up as described above. About 30 females were randomly selected from the mating jars each day at 1, 2, 3, 4, and 5 days after eclosion for 12 h of tethered flight on flight mills. Flight activity was not recorded but has been characterized in previous flight mill studies and is extensive at these ages (Jiang and Luo, 1998b). After tethered flight, the tether attached to adult dorsal surface was carefully cut away and each female was returned to its original jar with its male partner and permitted to oviposit until death. Twenty-five pairs of untethered adults were used as controls. The number of eggs laid by females and mortality were checked daily. Mating status and mating frequency were recorded after death by observing the number of spermatophores harbored by the female.

The second experiment was designed to examine the influence of mating status, mating frequency and fecundity on flight performance at different ages. Approximately 500 recently eclosed adults were divided into three groups, namely virgin females, virgin males and male–female pairs reared at densities of 2 individuals per 850-mL jar and provided with 5% honey solution. About 30 individuals of each group of virgins and 64 individuals (32 females and 32 males) from mated pairs were randomly selected at each of 2, 3, 5, and 7 days after eclosion for 12 h of tethered flight on flight mills. After tethered flight, all females of the mated group were dissected immediately to determine mating frequency by counting the number of spermatophores in the abdomen; total fecundity was determined by adding the number of eggs remaining in the ovaries to the cumulative number of eggs oviposited before tethered flight.

For each treatment, validated data from at least 18 (the first experiment) and 21 (the second experiment) adults were obtained. Data were excluded from the analyses if the adult was detached from the tether or broke a wing during the test period.

2.3. Flight test

Flight tests were conducted on a 32-channel flight mill system, as described in previous studies (Luo et al., 1995, 1999; Jiang and Luo, 1998b, 2005; Jiang, 1999; Jiang et al., 1999, 2000, 2002). To

facilitate attachment of tethers, the moths were lightly anaesthetized in a glass tube (2 cm × 8 cm) containing an ether-soaked cotton wick. The tether consisted of a 0.25-mm (diameter) copper wire with a 1-mm (diameter) loop at one end and a 2-cm straight portion of wire perpendicular to the loop. The loop was attached to the dorsal surface of the junction between the metathorax and the abdomen with 502-superglue (Aibida Adhesive Co., Guangdong, China) after the scales and hairs at the attachment site were removed with a brush. The tethered moth was held in a 50-mL vial until attachment to the arm of the flight mill system. Flight parameters, including total distance, total duration, and average velocity were automatically recorded by the system. The flight tests were performed in a climate chamber. Temperature and humidity in the flight room were maintained at 24 ± 1 °C and $70 \pm 10\%$ RH, respectively, conditions promoting maximum flight capacity of *S. exigua* (Jiang et al., 2002). Data logging (software supported by Jiaduo Co., Henan, China) began at 20:00 h in the evening and terminated at 08:00 h the next morning under dark conditions. This period is similar to that when actual migration of *S. exigua* occurs in the field (Feng et al., 2003).

2.4. Data analysis

All data obtained from the studies are presented as means ± SEM. Treatment effects on variables were evaluated by one-way analysis of variance (ANOVA). If the ANOVA indicated a significant difference, the means responsible for that difference were identified using a multiple means test. To test for effect of flight on reproduction and longevity, LSD was chosen because of its enhanced power to detect differences. Our presumption in this experiment was that if this species has no oogenesis-flight syndrome, there would be no differences between control moths and moths more than 2 days old. Because of its power to detect differences, an LSD showing no differences increases confidence that no true differences exist. However, to test for effects of mating frequency on 7-day-old moth flight, Tukey's HSD was used because we had no preconceived expectations about treatment effects. This test is more conservative than the LSD test in detecting differences between multiple means, so when significant differences are detected, we can be more confident that they are real. Differences in the flight parameters, including total distance, total duration, and average velocity between the virgin and mated moths at the same age were evaluated by independent sample *t*-tests. Relationships between females' fecundity and mating frequency, fecundity and measures of flight performance, as well as mating frequency and flight performance at days 3, 5 and 7 after eclosion in the second experiment were analyzed with Pearson correlation coefficients (Zar, 2009). All statistical procedures were performed with SPSS software (SPSS 17.0).

3. Results

3.1. Influence of flight on reproduction

The pre-oviposition period, oviposition period, number of eggs laid per female, mating percentage and frequency, and the

longevity of *S. exigua* investigated after 12 h tethered flight on a flight mill are presented in Table 1. Tethered flight did not decrease lifetime female reproductive output compared to controls except when they were flown the first day after eclosion (Table 1). In addition, those flown at 1 day old had a significantly prolonged pre-oviposition period, decreased oviposition period, decreased longevity, and decreased lifetime mating frequency compared to controls and those flown at 2–5 days old (Table 1). In contrast, these parameters did not differ significantly among those flown during the inter-oviposition period from day 2 to day 5 after eclosion and unflown controls (Table 1). Although females flown on the fifth day after eclosion had significantly decreased total fecundity compared to the control (Table 1), the negative trends in their pre-oviposition period, oviposition period, mating rate, mating frequency and longevity were not statistically significant.

3.2. Influence of mating status on flight

Adults were further tested to determine if they have enough flight capacity to pursue inter-ovipositional migratory flights by comparing flight performance of virgin and mated moths at different ages. Mating status did not influence flight of either sex at most ages tested (Fig. 1). No significant differences were observed in flight distance, flight velocity and flight duration between virgin and mated moths of the same age from 2 to 5 days old regardless of sex (Fig. 1). However, 7-day-old mated females had significantly lower average flight distance ($t = 2.67$; $df = 53$; $P = 0.01$) and flight duration ($t = 2.54$; $df = 53$; $P = 0.01$) than virgin females, but there was no difference in average flight velocity ($t = 1.66$; $df = 53$; $P = 0.10$). In contrast, no significant differences in average flight distance ($t = 0.74$; $df = 53$; $P = 0.94$), flight velocity ($t = 0.82$; $df = 53$; $P = 0.42$) and flight duration ($t = 0.034$; $df = 53$; $P = 0.97$) were observed between virgin and mated males.

3.3. Influence of mating frequency on flight

To explore the reason why female flight performance decreased significantly by 7 days, we analyzed the influence of mating frequency in 7-day-old moths on flight performance (Fig. 2). Accumulated matings by females of this age was associated with a decrease in flight performance (Fig. 2). Mating frequency was significantly negatively correlated with flight distance and flight duration, but the negative correlation between mating frequency and flight velocity was not significant (Table 2). Females mated more than 4 times exhibited significantly lower flight distance, flight velocity and flight duration than virgins (Fig. 2). Flight performance of virgin 7-day-old females and females mated only 1–4 times did not differ significantly. In contrast, 7-day-old males that had mated more than 4 times exhibited significantly higher mean flight distance and flight duration than those mated 1–4 times, but there was no significant difference in flight velocity (Fig. 2).

Table 1

Influence of moth flight at different ages on fecundity, mating success and longevity of female *S. exigua*. Data are presented as means ± SEM. In each column, data sharing the same letter are not significantly different at the 5% level by LSD.

Age at time of flight (days)	Samples (n)	Pre-oviposition period (days)	Oviposition period (days)	Total no. of eggs laid in lifetime	Mating percentage (%)	Mating frequency (spermatophores per female)	Female longevity (days)
Control (no flight)	21	2.19 ± 0.11 a	6.57 ± 0.68 a	758.38 ± 43.14 a	100.0	3.43 ± 0.31 a	10.10 ± 0.64 a
1	20	3.45 ± 0.15 b	3.10 ± 0.35 b	590.40 ± 41.34 b	95.0	2.30 ± 0.18 b	6.85 ± 0.49 b
2	18	2.61 ± 0.12 a	7.33 ± 0.54 a	673.72 ± 42.73 ab	94.4	3.22 ± 0.42 a	11.22 ± 0.69 a
3	23	2.48 ± 0.19 a	6.83 ± 0.44 a	633.30 ± 55.24 ab	95.7	3.39 ± 0.30 a	10.61 ± 0.64 a
4	21	2.57 ± 0.22 a	6.24 ± 0.47 a	621.90 ± 60.99 ab	95.2	3.33 ± 0.37 a	10.71 ± 0.86 a
5	20	2.25 ± 0.09 a	6.10 ± 0.42 a	565.15 ± 32.68 b	100.0	3.40 ± 0.28 a	9.90 ± 0.53 a

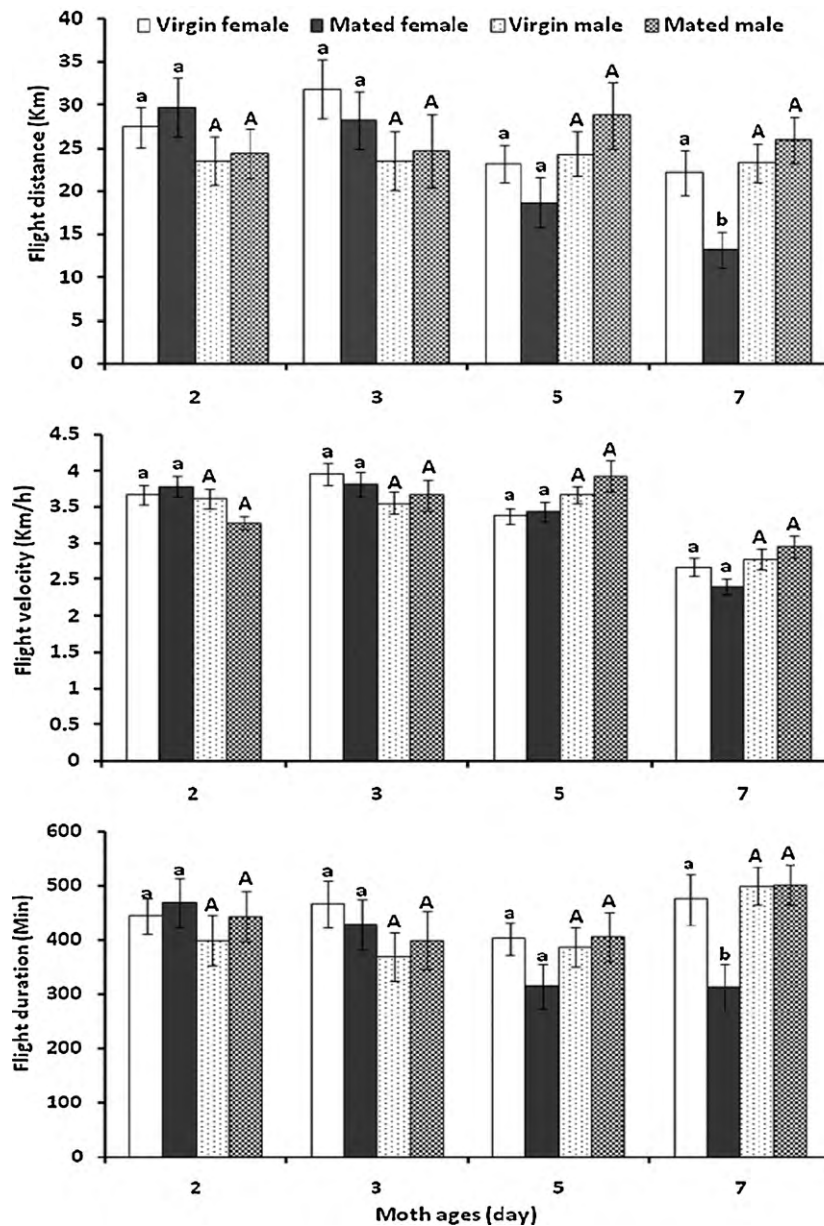


Fig. 1. Comparison of flight performance between virgin and mated females and males of *S. exigua* at indicated ages. Means (\pm SEM) with the same letters within sex (females lower case and males upper case) and age are not significantly different ($P > 0.05$). Sample sizes from left to right are 22, 24, 24, 23, 28, 22, 22, 21, 30, 26, 30, 32, 28, 27, 26 and 29, respectively.

3.4. Correlation among egg laying, mating frequency and flight

Because of the lack of differences in flight performance by mated and virgin females at both 3 and 5 days old, the time of peak oviposition (Tisdale and Sappington, 2001), and at a time when multiple mating occurred, we expected no negative relationship between the number of eggs produced or mating frequency and flight performance. In fact, there were no significant correlations between eggs produced and flight distance, velocity and duration for both 3 and 5-day-old females (Table 3), a finding supported by the results of Han et al. (2008). Even among 7-day-old females, which showed a moderate negative correlation between the number of eggs produced and flight distance and duration, there was no significant correlation when females that mated 4 times or less were grouped for analysis (Table 3). Owing to a significant positive correlation between the number of eggs produced and mating frequency at 3 ($r = 0.87$, $P < 0.01$), 5 ($r = 0.79$, $P < 0.01$), and 7 ($r = 0.91$, $P < 0.01$) days old, the correlations between female

mating frequency and flight (Table 2) showed the same tendency as those observed between the number of eggs produced and flight performance (Table 3).

4. Discussion

The basic characteristics of migration, overwintering and reproduction in *S. exigua*, as well as possible environmental and physiological factors influencing them, have been well-analyzed in our previous studies (Jiang and Luo, 1998b, 1999; Jiang, 1999; Jiang et al., 1999, 2000, 2001, 2002). However, migratory behavior as it relates to reproduction, which in some insects takes the form of the oogenesis-flight syndrome, has not been well-examined. In some insects, it is possible to accurately estimate migratory population dynamics and the emigrant and immigrant status of populations by determining adult ovarian development (Jiang and Luo, 2005). Thus, it is important to understand the relationship between migration and reproduction in *S. exigua*, because it governs if and

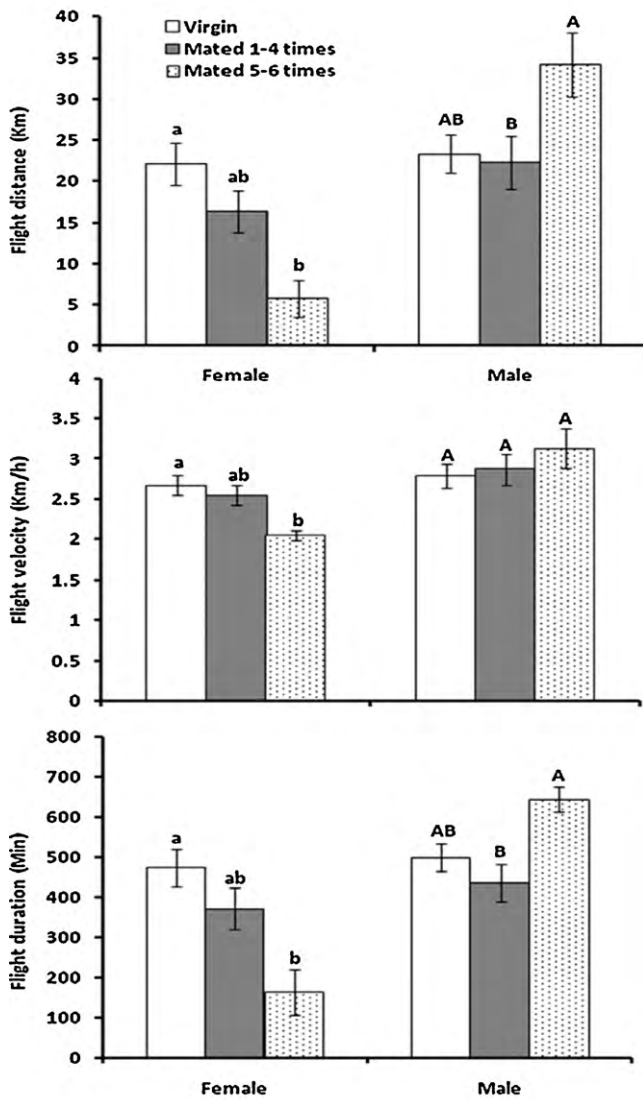


Fig. 2. Comparison of flight performance among 7-day-old female and male *S. exigua* that was virgin, mated 1–4 times and mated 5–6 times. Means (\pm SEM) with the same letters within sex (females lower case and males upper case) are not significantly different by Tukey's HSD ($P > 0.05$). Sample sizes from left to right are 28, 19, 8, 26, 19 and 10, respectively.

how ovarian development can be used as a tool in population forecasting.

The presence of an oogenesis-flight syndrome in *S. exigua*, in which the insect exhibits pre-ovipositional migration and negative effects of post-ovipositional flight on reproduction (Luo et al., 1999), is not supported by our study. First, inter-ovipositional flight on flight mills did not exact a reproductive cost. In fact, flight

Table 2

Pearson correlation coefficients between mating frequency and flight performance of *S. exigua* females at different ages after eclosion.

Age	Mating frequency	Sample size	Flight distance		Flight velocity		Flight duration	
			<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
3	1–4	22	0.12	0.61	0.13	0.56	0.06	0.78
5	1–4	26	0.18	0.37	0.15	0.46	0.08	0.72
7	1–4	19	–0.14	0.57	0.04	0.86	–0.18	0.46
	1–6	27	–0.45	0.02*	–0.32	0.10	–0.45	0.02*

* Correlation is significant at the 0.05 level.

Table 3

Pearson correlations coefficients between number of eggs produced and flight performance of mated *S. exigua* females at different ages after eclosion.

Age	Mating frequency	Sample size	Flight distance		Flight velocity		Flight duration	
			<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
3	1–4	22	–0.07	0.76	0.14	0.52	–0.19	0.41
5	1–4	26	–0.06	0.77	0.03	0.89	–0.20	0.32
7	1–4	19	–0.07	0.79	0.18	0.46	–0.12	0.13
	1–6	27	–0.42	0.03*	–0.31	0.12	–0.42	0.03*

* Correlation is significant at the 0.05 level.

by pre-ovipositional 1-day-old females had a negative effect on lifetime egg production and longevity. Beet armyworm moths of this age average 5.5 h of flight on flight mills, which is substantial but considerably less than that of 2–5-day-old moths (9.5–10.7 h) (Jiang and Luo, 1998b). Thus, it is possible that underdeveloped flight muscles or other tissues of 1-day-old moths were overtaxed and damaged during the strenuous activity of flight. More likely, however, is that because fecundity and longevity are optimal when females mate on the first or second day after eclosion (Rogers and Marti, 1996, 1997; Jiang, 1999), an important mating opportunity was lost on the first night by being tethered to a flight mill, perhaps compounded by a second night of recovery. Secondly, the mating status of both females and males had no negative influence on their flight performance up to 7 days old. This is not consistent with the oogenesis-flight syndrome observed in many other migratory insects, which show a temporary suppression of sexual behavior during the migratory period and a sharp decrease in flight capacity after mating (e.g., Armes and Cooter, 1991; Colvin and Gatehouse, 1993). Thirdly, the number of eggs laid and mating frequency by females up to 7 days of age was not correlated with flight performance, suggesting a parallel and independent development of flight and reproductive systems. Migratory insects exhibiting the oogenesis-flight syndrome display a negative correlation in timing of flight and reproduction and a decrease in flight activity with increasing number of eggs laid (Luo et al., 1995). Finally, a very short pre-oviposition period in *S. exigua* has been observed in this and previous studies, indicating that resources for adult reproduction are committed during the pupal stage. A similar pattern is found in the whitefly parasitoid *Eretmocerus eremicus*, a migratory insect in which the oogenesis-flight syndrome is also absent (Bellamy and Byrne, 2001; Asplen et al., 2009).

Given the clear absence of the oogenesis-flight syndrome in *S. exigua*, we propose instead a conceptual migratory model for this species based on the results of this and previous studies. Migratory behavior probably is initiated during the oviposition period from 2 to 7 days post-eclosion, rather than on the first day of the pre-oviposition period, and after initial mating on the first night. The logic supporting this is that adults on the first day after eclosion are relatively poor fliers (Jiang and Luo, 1998b; Jiang, 1999), perhaps because they need time to fully develop their flight apparatus, and this is the most critical age to mate. Otherwise, young females suffer reduced lifetime reproductive output by losing early mating opportunities, which in turn results in a prolonged pre-oviposition period and decreased lifetime egg production (Rogers and Marti, 1996, 1997). Conversely, flight on days 2–7 during the oviposition period had no significant negative effect on reproduction. Timing of migration to begin during the longer oviposition period, rather than being confined to the much shorter pre-oviposition period, may improve the flexibility of this life history strategy in the face of uncertain environmental conditions. It would extend the option for individuals to escape unfavorable conditions and to exploit new habitat across a wide temporal window (Southwood, 1962; Lidicker and Caldwell, 1982; Rankin and Singer, 1984).

Unlike migratory insects exhibiting the oogenesis-flight syndrome (Rankin et al., 1986, 1994; Colvin and Gatehouse, 1993; Keil et al., 2001; Gu et al., 2006; Lorenz, 2007), we hypothesize that *S. exigua* pursues multiple matings during the migratory phase and that it oviposits part of its eggs en route. Supporting this is that mating frequency and the numbers of eggs laid up to 7 days post-eclosion have no negative influence on flight performance, which is consistent with synchronous migratory behavior. Oviposition during migration is exhibited by, for example, migrating monarch butterflies, *Danaus plexippus* L. (Brower, 1996), and probably the common green darner, *Anax junius* (Drury) (Russell et al., 1998). It is a bet-hedging evolutionary life history strategy for colonization of habitats that are unpredictable or spatially spread out (Holland et al., 2006). During inter-ovipositional migration, female reproductive risk and intraspecific competition can be reduced by laying eggs in widely separated locations (McAnelly and Rankin, 1986). Resumption of migratory flight can also be a facultative response to an environment unfavorable to adult longevity (Dingle, 1972; Rankin and Riddiford, 1977; Rankin and Singer, 1984; McAnelly and Rankin, 1986). However, our results suggest that the accumulation of more than four matings and oviposition of high numbers of eggs up to day 7 may serve as signals to terminate migratory behavior. Flight performance decreases rapidly after 7 days of age (Jiang and Luo, 1998b; Jiang, 1999), and both accumulated matings and the number of eggs laid by females at this age were significantly negatively correlated with flight performance (Tables 2 and 3).

Our hypotheses related to the migratory model we propose for *S. exigua*, given the absence of the oogenesis-flight syndrome, are based mainly on laboratory studies, and more intensive field observations as well as laboratory studies of the mechanisms regulating migration are needed to test them further. Our previous studies on the physiological regulation of migration in this species demonstrated that lipid, including glyceride, is the most important energy fuel for long-distance sustained migratory flight (Li et al., 2005). Field observations of adults feeding on plant nectar and honeydew, which can be transformed into lipid fuel before migration, suggest adult feeding may be a strategy to maintain strong flight performance during the oviposition period without sacrificing lifetime fecundity (Yu and Cheng, 1989). For example, intake of carbohydrate by adult African armyworm, *Spodoptera exempta* (Walker), can mitigate the trade-off between migratory flight and reproduction (Gunn et al., 1989). Laboratory studies will be necessary to determine whether and at what point supplementary energy intake by *S. exigua* adults is a restrictive condition for successful migration (Jiang et al., 2000). Finally, this species should provide a good model to explore the mechanisms integrating the metabolic and physiological aspects of synchronous reproduction and migration in migratory insects lacking the oogenesis-flight syndrome.

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