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Abstract

The beet webworm, *Loxostege sticticalis* (L.) (Lepidoptera: Pyralidae), uses both diapause and migration as life history strategies. To determine the role of diapause plays in the population dynamics of *L. sticticalis*, the reproductive and flight potentials of adults originating from diapause and nondiapause larvae were investigated under controlled laboratory conditions. Preoviposition period, lifetime fecundity, and daily egg production of females originating from diapause larvae were not significantly different from those originating from nondiapause larvae, showing that diapause has no significant effect on reproductive capacity when adults are provided with an adequate carbohydrate source. However, females that developed from diapause larvae lived significantly longer than those from nondiapause larvae. Flight capacity, including flight duration, distance and velocity of 3-d-old adults were all significantly greater in adults originating from diapause larvae than those from nondiapause larvae. *L. sticticalis* adults developing from diapause larvae tended to have more extreme values of longest flight duration and furthest flight distance than those from nondiapause larvae. Together, these results suggest that long-distance flight potential of *L. sticticalis* is greater after larval diapause than after direct development to adulthood. However, there were no significant differences between sexes within the two categories of moths in terms of total flight duration, total flight distance, flight velocity, and longest flight duration.

Keywords

Loxostege sticticalis, diapause, reproduction, flight

Disciplines

Agriculture | Animal Sciences | Biology | Comparative and Evolutionary Physiology | Entomology | Structural Biology

Comments

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ABSTRACT The beet webworm, *Loxostege sticticalis* (L.) (Lepidoptera: Pyralidae), uses both diapause and migration as life history strategies. To determine the role of diapause plays in the population dynamics of *L. sticticalis*, the reproductive and flight potentials of adults originating from diapause and nondiapause larvae were investigated under controlled laboratory conditions. Preoviposition period, lifetime fecundity, and daily egg production of females originating from diapause larvae were not significantly different from those originating from nondiapause larvae, showing that diapause has no significant effect on reproductive capacity when adults are provided with an adequate carbohydrate source. However, females that developed from diapause larvae lived significantly longer than those from nondiapause larvae. Flight capacity, including flight duration, distance and velocity of 3-d-old adults were all significantly greater in adults originating from diapause larvae than those from nondiapause larvae. *L. sticticalis* adults developing from diapause larvae tended to have more extreme values of longest flight duration and furthest flight distance than those from nondiapause larvae. Together, these results suggest that long-distance flight potential of *L. sticticalis* is greater after larval diapause than after direct development to adulthood. However, there were no significant differences between sexes within the two categories of moths in terms of total flight duration, total flight distance, flight velocity, and longest flight duration.

KEY WORDS *Loxostege sticticalis*, diapause, reproduction, flight

Diapause is a dynamic adaptation to arrest development at a specific stage for a given species (Andrewartha 1952; Dingle 1978; Tauber et al. 1986; Hodek 1996, 2002). As a distinct life history strategy, diapause enables the species to synchronize their life cycles to the seasons and the host plants (Masaki 1980, Hodek 2002), and plays an important role in population dynamics. In addition, the effects of diapause on life history traits after its termination may also influence population dynamics of a species. For example, several studies indicated that diapause may incur a cost. That is, individuals that have experienced diapause phase may have lower egg production, shorter adult longevity, or both compared with individuals originated from a nondiapausing population (Williams 1966, Gebre-Amlak 1989, Ishihara and Shimada 1995, Kroon and Veenendaal 1998, Saunders 2000, Eilers and Van Alphen 2002). Such phenomena represent a trade-off

between diapause and other life history traits (Roff 1992). However, in a few species, diapause in an immature stage is positively correlated with fecundity of the resultant adults (Spence 1989, Fantinou et al. 2004, Wang et al. 2006b).

Migration is also an important adaptation to temporary habitat patches that vary in availability and quality both in space and time (Southwood 1977). By determining where and when reproduction occurs, migration has a major influence on adult fitness. Migration is thus a fundamental component of the life histories for migratory species and plays a key role in their population dynamics (Dingle 1984). However, effects of overwintering diapause of immature stages on the subsequent flight capacity of adults are poorly understood at present. Evidence of research from Lepidoptera species (Van Dyck and Wiklund 2002, Fric et al. 2006, Sarvary et al. 2008), suggesting that adults that experienced diapause as larvae may differ in flight performance from those that developed directly to adulthood. Therefore, investigation of the reproductive and flight capacity of the postdiapause population will be of great importance in fully understanding the population dynamics of relevant species.

The beet webworm, *Loxostege sticticalis* (L.) (Lepidoptera: Pyralidae), which overwinters as a diapausing mature larva, is a serious economic pest of crops

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and fodder within a belt zone from 36° N to 55° N in China (Pepper 1938, Knor et al. 1993, Luo 2004, Luo et al. 2009). Unlike other seasonal migrants, the beet webworm can survive only in areas where the larvae can enter diapause, because reproduction and distribution of adult *L. sticticalis* are greatly limited by temperature and precipitation (Pepper 1938). Larval diapause is the only life history strategy that can carry a population through the winter. Diapause of *L. sticticalis* is regulated by both photoperiod and temperature (Goryshin et al. 1980, Omelyuta 1981, Tian and Gao 1986, Chen et al. 1987, Huang et al. 2009). The mature larva continues development under a photoperiod of 16:8 (L:D) h, but enters diapause when the photoperiod is <16 h. Temperature, food plant, and larval density also have a significant effect on diapause rate of the mature larvae (Khomyakova et al. 1986, Tian and Gao 1986, Knor et al. 1993).

Reproduction and migration are the biological characteristics of moths, which influence the occurrence and damage of the resultant populations. The beet webworm can complete two or three generations annually in northern China (Luo and Li 1992, Luo and Qu 2005), but substantial economic damage is caused mainly by first-generation larvae, whose populations are directly affected by the fecundity of adults developed from the diapausing larvae. Migration is then one of the principal factors determining where outbreaks of *L. sticticalis* occur. Evidence from behavioral characterization of migratory movement (Chen et al. 1992, Luo and Li 1992, Feng et al. 2004, Sun and Gao 2004, Cao et al. 2006); coupled with elucidation of migratory routes (Sun and Chen 1995, Chen et al. 2004, Cao et al. 2006, Zhang et al. 2008); distance and causes (Sun and Chen 1995, Qu et al. 1999, Jiang et al. 2010a), indicate that the flight potential of this long-range migratory pest has an impact on areas, which are at risk of damage in a given year. Migration may occur when the mass emergence period of overwintering adults is not synchronized with host phenology at the overwintering site (Chen and Yang 1999), but little is known about the flight activity of the overwintered generation. Therefore, it is of great importance to compare reproductive and flight capacity of adults originating from diapause and nondiapause larvae, which helps to understand the role of diapause in population dynamics.

In the current study, we tested the hypothesis that costs are associated with diapause in *L. sticticalis*, which provides an excellent experimental model to investigate the influences of diapause on future reproduction and migration. The effects of diapause on reproduction and flight capacity of *L. sticticalis* of the overwintered generation were measured under laboratory conditions, and flight performance of males and females derived from diapause and nondiapause larvae were investigated. This information is essential to the development of a theoretical foundation for managing overwintering populations and for improving forecasts of the population dynamics of this pest.

Materials and Methods

Insect Rearing. A laboratory population of *L. sticticalis* was established by collecting diapausing larvae from the field in Siziwangqi (41° 53' N, 111° 70' E) of Inner Mongolia, China in 2008. Larvae were reared in a climatic chamber (RXZ-430B; Ningbo, China) at 22 ± 1°C, 70–80% RH, and a photoperiod of 16:8 (L:D) h until pupation and adult emergence. Adults emerging on the same day were collected and kept together in a 1.5-liter plastic cage for mating and oviposition. Adults were provided with 10% glucose solution (wt: vol) as supplemental food, which was renewed daily, and their eggs were laid in the plastic cage on gauze. Larvae were maintained in 500-ml beakers and fed daily with fresh leaves of lambsquarters, *Chenopodium album* L. When larvae stopped feeding, sterilized soil containing ≈10% water was added to the bottom of the beakers to a depth of around 5 cm, which provided a substrate for cocoon formation, pupation, and adult emergence.

Obtaining Diapause and Nondiapause Populations. Insects of the parental generation were reared under the above conditions of 16:8 (L:D) h at 22°C with fresh leaves of lambsquarters. Newly hatched larvae produced by these parents were reared at a density of 10 larvae per 500-ml beaker and divided into two groups. To induce diapause, one group was kept in a climatic chamber at 22 ± 1°C, 75% RH, and a photoperiod of 12:12 (L:D) h (light intensity during the photoperiod was ≈6,000 lux). Under these conditions, 98–100% of mature larvae entered diapause (Huang et al. 2009). Diapausing larvae (≈150) were placed in a refrigerator and held at 0°C (BCD-261EA; Electrolux, China) for 5 mo to simulate winter field conditions. They then were transferred to environmental chambers at 22 ± 1°C with a photoperiod of 16:8 (L:D) h until pupation and adult emergence. To obtain nondiapause larvae, another group was maintained continuously in a chamber at 22 ± 1°C, 75% RH, and a photoperiod of 16:8 (L:D) h until pupation and adult emergence.

Determination of Reproductive Capacity. Newly emerged adults were paired in plastic cages (1.5 liters). Each male–female pair comprising a replicate was provided with a 10% glucose solution (wt: vol). Twenty-five and 24 pairs of adults originating from diapause and nondiapause larvae, respectively, were kept in a chamber under 122°C, 75% RH, and a photoperiod of 16:8 (L:D) h. Preoviposition period, oviposition period, mean lifetime egg production, mean daily egg production per female, and the longevity of females and males were recorded. Data were excluded from the analyses if either males or females escaped during the experiment. The experiments were terminated when all of the males and females had died.

Determination of Flight Potential. Flight activity of *L. sticticalis* originating from diapause and nondiapause larvae was monitored by a computer-aided flight information system (Jiaduo Science, Industry and Trade Co., Henan, China), as described in previous studies (Luo and Li 1992, Luo et al. 2002). Flight tests were conducted on a 24-channel flight mill sys-

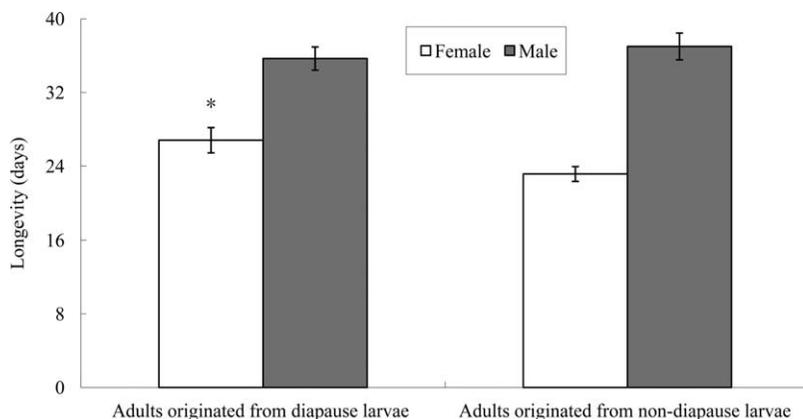


Fig. 1. Comparison of longevity of *L. sticticalis* adults originating from diapause and nondiapause larvae at 22°C, 75% RH, and a photoperiod of 16:8 (L:D) h. Sample sizes for adults originating from diapause and nondiapause larvae were 22 and 24 pairs, respectively. Data are presented as means \pm SE. Asterisk indicates means for females originating from diapause and nondiapause larvae differed significantly (*t*-test, $*P < 0.05$).

tem. The flight mill arm was made of a special alloy wire (0.03 cm in diameter, 15 cm long) and mounted to permit horizontal revolutions with very little friction by using magnetic suspension.

Three-day-old unmated females and males originating from diapause or nondiapause larvae were selected for testing, because 1- and 2-d-old adults exhibit lower flight activity (Luo and Li 1992). Test moths with forewing lengths ranged from 2.2 to 2.6 cm were selected for the experiments and tethered. To facilitate attachment of tethers, the adults were lightly anesthetized for 4–5 s by placing each inside a glass tube (1.5 by 7 cm) containing an ether-soaked cotton wick. The tether consisted of an alloy wire with a 1-mm (diameter) loop at one end and a 1.5-mm straight portion of wire perpendicular to the loop. The loop was attached to the mesothorax with 502 superglue (Chuanghui Adhesive Co., Shenzhen, China) after the scales and hairs at the attachment site were removed with a soft brush. The anesthesia, measurement of wings, and tethering the moths took place in light. After tethering, the moths were subjected to 60 min acclimatization to the darkness, transferred to a dark climate-control chamber and attached to the flight mill arm. The tests were performed in darkness, at $20 \pm 1^\circ\text{C}$ and 70–80% RH, conditions promoting maximum flight capacity of *L. sticticalis* (Luo and Li 1992). Data were recorded from 1930 to 0730 hours of local time, the time corresponding to the period of mass flight of *L. sticticalis* in the field (Feng et al. 2004). Approximately 60 adults were observed for each treatment. Adults were excluded from the data analyses if they were found detached from the tether or with a broken wing after the test period. In addition, data from moths with total flight duration < 30 min were discarded, because it is possible that low flight activity is an artifact of handling or trauma during the tethering process.

Flight capacity of *L. sticticalis* was characterized using the standards of Luo et al. (2002). Flight parameters, including total flight duration and distance,

average velocity, longest flight duration, and furthest flight distance were recorded automatically by the system. Longest flight duration and furthest flight distance were those of the single longest uninterrupted flight.

Data Analysis. All data were checked for fit to a normal distribution by using the Kolmogorov–Smirnov test, implemented in SPSS 11.0 (SPSS 1999). The reproductive and flight parameters of adults originating from diapause and nondiapause larvae were measured by independent-samples *t*-test. All values obtained from the studies are presented as means \pm SE. The differences of the flight parameters were analyzed further by comparing the frequency distribution of longest flight duration and furthest flight distance between the two categories of moths by using a procedure for two sample *t*-test between percents available at <https://www.statpac.com/statistics-calculator/percents.htm#D2HTopicM13>.

Results

Reproductive Capacity. There were no significant differences in the preoviposition period ($t = 1.000$, $df = 44$, $P = 0.323$); oviposition period ($t = 0.382$, $df = 44$, $P = 0.704$); lifetime egg production per female ($t = 0.376$, $df = 44$, $P = 0.709$); mean daily egg production per female ($t = 0.442$, $df = 44$, $P = 0.661$); and the longevity of males ($t = 0.681$, $df = 44$, $P = 0.500$; Fig. 1) among adults originating from diapause or nondiapause larvae. However, longevity of female adults originating from diapause larvae was significantly longer than that of female adults from nondiapause larvae ($t = 2.308$, $df = 44$, $P = 0.026$; Fig. 1) under laboratory conditions.

Flight Potential. Data from adults originating from diapause and nondiapause larvae were examined by gender. There were no significant differences between males and females in total flight duration (diapause: $t = 0.326$, $df = 43$, $P = 0.746$; nondiapause: $t = 0.580$, $df = 38$, $P = 0.566$); total flight distance (dia-

Table 1. Flight capacity parameters of 3-d-old *L. sticticalis* developing from diapause and nondiapause larvae during a 12-h tethered-flight test

Origin	Gender	No. of individuals	Total flight duration (h)	Total flight distance (km)	Flight velocity (km/h)	Longest flight duration (h)
Adults developing from diapause larvae	Female	25	7.74 ± 0.63	27.09 ± 3.16	3.36 ± 0.20	4.60 ± 0.64
	Male	20	8.05 ± 0.72	27.14 ± 3.14	3.21 ± 0.22	5.82 ± 0.65
Adults developing from nondiapause larvae	Female	19	5.62 ± 0.74	12.68 ± 2.91	2.67 ± 0.19	2.83 ± 0.41
	Male	21	6.26 ± 0.79	17.58 ± 3.00	2.56 ± 0.19	2.64 ± 0.43

There were no significant differences between sexes within origin for any of the parameters measured ($P > 0.05$) as determined by independent-samples *t*-test. Data are presented as means ± SE.

pause: $t = 0.010$, $df = 43$, $P = 0.992$; nondiapause: $t = 0.279$, $df = 38$, $P = 0.782$); average flight velocity (diapause: $t = 0.497$, $df = 43$, $P = 0.622$; nondiapause: $t = 0.415$, $df = 38$, $P = 0.680$); and longest flight duration (diapause: $t = 1.325$, $df = 43$, $P = 0.192$; nondiapause: $t = 0.310$, $df = 38$, $P = 0.759$) (Table 1). Therefore, male and female data were pooled for subsequent analyses.

Significant differences were observed in flight potential between adult *L. sticticalis* developing from

diapause and nondiapause larvae (Fig. 2). Adults originating from diapause larvae showed significantly greater total flight duration ($t = 2.696$, $df = 83$, $P = 0.008$; Fig. 2A); total flight distance ($t = 3.298$, $df = 83$, $P = 0.001$; Fig. 2B); and velocity ($t = 3.457$, $df = 83$, $P = 0.001$; Fig. 2C). These differences were analyzed further by comparing the frequency distribution of longest flight duration and furthest flight distance between the two categories of moths (Fig. 3). A large proportion of adults originating from diapause larvae

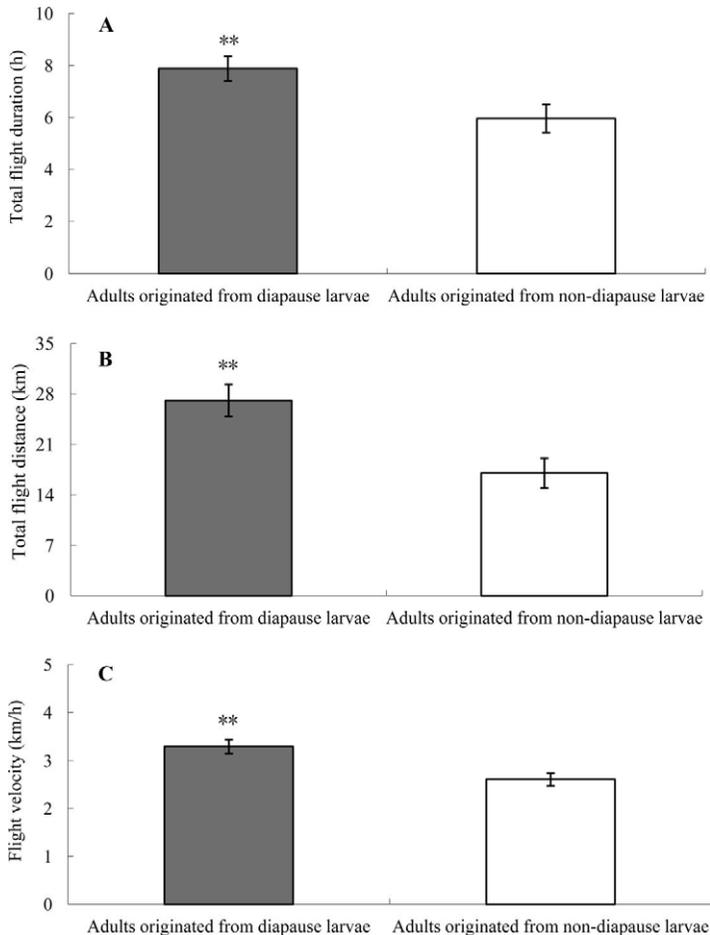


Fig. 2. Total flight duration (A), total flight distance (B), and mean flight velocity (C) of 3-d-old *L. sticticalis* adults during a 12-h tethered-flight test. Sample sizes for flight treatments of adults originating from nondiapause and diapause larvae were 40 and 45, respectively. Data are presented as means ± SE. Asterisks indicate means are significantly different (*t*-test, $**P < 0.01$).

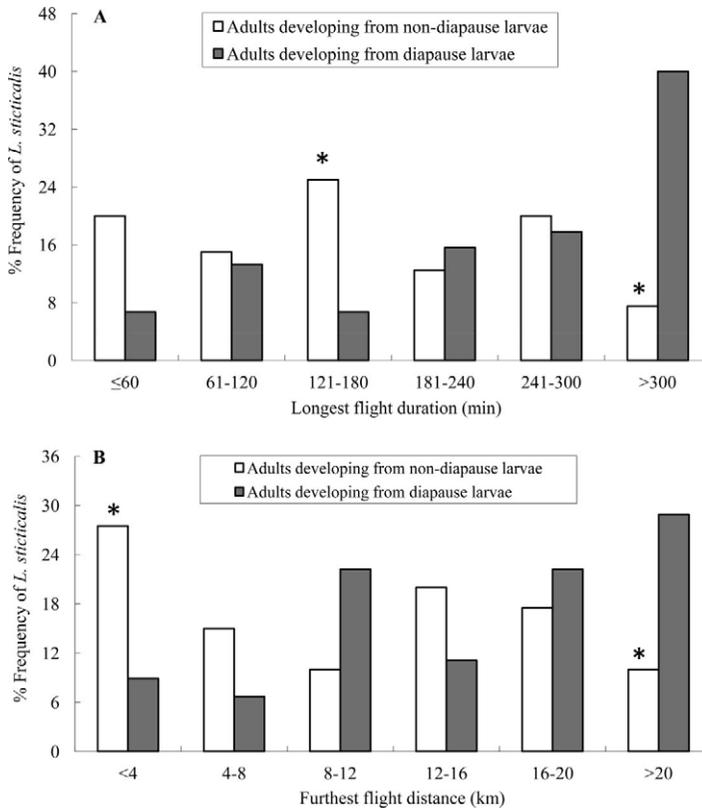


Fig. 3. Frequency (percentage) distribution of longest flight duration (A) and furthest flight distance (B) of 3-d-old *L. sticticalis* during a 12-h flight mill test. Sample sizes for flight treatments of adults originating from nondiapause and diapause larvae were 40 and 45, respectively. Asterisks indicate percentage are significantly different (*t*-test, **P* < 0.05).

(*n* = 45) engaged in long-duration flight, with 73.3 and 40%, making a continuous flight >3 h and >5 h, respectively, during the 12-h test period (Fig. 3A). In contrast, only 40 and 7.5% of adults originating from nondiapause larvae (*n* = 40) flew >3 h and >5 h, respectively. Only 6.7% of adults originating from diapause larvae did not make a long-duration flight >1 h, whereas 20% of adults originating from nondiapause larvae flew ≤1 h. Similarly, *L. sticticalis* adults developing from diapause larvae tended to have more extreme values of furthest single flight distance than those from nondiapause larvae (Fig. 3B), with 51.1% versus 27.5%, respectively, flying >16 km. Therefore, although adults of both groups were capable of long-duration and long-distance flights, those originating from diapause larvae displayed greater flight potential on the flight mill system. These differences were analyzed further by comparing the frequency distribution of longest flight duration and furthest flight distance between the two categories of moths (Fig. 3). A large proportion of adults originating from diapause larvae (*n* = 45) engaged in long-duration flight, with 73.3 and 40%, making a continuous flight >3 h and >5 h, respectively, during the 12-h test period (Fig. 3A). In contrast, only 40 and 7.5% of adults originating from nondiapause larvae (*n* = 40) flew >3 h and >5 h, respectively. There were significant differences be-

tween the percents of adults that flew >3 h (*t* = 3.101, *df* = 83, *P* = 0.003) and >5 h (*t* = 3.468, *df* = 83, *P* = 0.008) originating from diapause and nondiapause larvae, respectively. Only 6.7% of adults originating from diapause larvae did not make a long-duration flight >1 h, whereas 20% of adults originating from nondiapause larvae flew ≤1 h, although the difference is no significant (*t* = 1.822, *df* = 83, *P* = 0.072). Similarly, *L. sticticalis* adults developing from diapause larvae tended to have significantly more extreme values of furthest single flight distance than those from nondiapause larvae (Fig. 3B), with 51.1% versus 27.5%, respectively, flying >16 km (*t* = 2.217, *df* = 83, *P* = 0.029). Therefore, although adults of both groups were capable of long-duration and long-distance flights, those adults originating from diapause larvae displayed greater flight potential on the flight mill system.

Discussion

For some insects, diapause has a negative effect on postdiapause adult life-history traits. In a multivoltine bruchid, *Kytorhinus sharpianus* Bridwell, fecundity of postdiapause females is less than that of females that developed from nondiapause larvae (Ishihara and Shimada 1995). In the spider mite, *Tetranychus urticae*

Koch, there is a negative correlation between diapause duration and postdiapause reproduction (longevity, total egg production, average oviposition rate) (Kroon and Veenendaal 1998). In the parasitoid wasp, *Asobara tabida* Nees, individuals that experienced diapause have lower fecundity and higher mortality than those that developed directly (Eilers and Van Alphen 2002). Such negative correlations between diapause and reproduction are often explainable by the partial depletion of metabolic reserves, which play an important role in diapause in many overwintering insects (Tauber et al. 1986, Danks 1987). Although diapause typically is characterized by decreased respiratory metabolism (Danks 1987, Guppy and Withers 1999), a low metabolic rate can draw heavily on nutrient reserves (Tauber et al. 1986).

However, not all species show diapause-associated costs in successive life history traits. For example, in the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), females that experience diapause show no apparent reduction in fecundity (Peferoen et al. 1981, Jansson et al. 1989, Ferro et al. 1991). Diapause even has been associated with greater fecundity in the grasshopper *Tetrix undulata* (Sow.) (Poras 1976); *Grapholita fumebrana* Tr. (Saringer and Szentkiralyi 1980); four pond skater species, *Gerris buenoi* Kirkaldy, *Gerris comatus* Drake and Hottes, *Gerris pingreensis* Drake and Hottes, and *Limnoporus dissortis* Drake and Harris (Spence 1989); and cabbage beetle *Colaphellus bowringi* Baly (Wang et al. 2006b). In the goldenrod gall fly *E. solidaginis*, larvae exposed to cold winter microenvironments had higher survival rates and postdiapause fecundity (Irwin and Lee 2002, 2003). The duration of diapause is also positively correlated with fecundity in the corn stalk borer *Sesamia nonagrioides* (Fantinou et al. 2004).

The relationship between diapause and reproduction was estimated in *L. sticticalis*. Mean total egg production and daily egg production of the females derived from diapause larvae were similar to those of females originating from nondiapause larvae. Moreover, adults originating from diapause larvae did not differ significantly in preoviposition and oviposition periods from adults derived from nondiapause larvae. Together, our results revealed no sublethal effects of diapause on reproductive capacity or longevity.

Among cold-tolerant insect species, low temperatures during diapause may promote significant energetic savings (Irwin and Lee 2002, 2003). The overwintering sites of *L. sticticalis* are generally located in northern areas of China around 36° N, where mild winter temperatures are typically below 0°C but can reach even lower than -20°C. Thus, low overwintering temperatures may reduce the energetic costs of diapause. Reduced cost of diapause at low temperatures has been confirmed in *Eurosta solidaginis* (Fitch) (Irwin and Lee 2002, 2003) and *Diplolepis spinosa* (Ashmead) (Williams et al. 2003), although the effect of low temperature on diapause maintenance is less well understood.

However, the relationship between diapause and reproductive costs may not be so simple in the case of

L. sticticalis. In contrast to our results, Jiang et al. (2010b) found that diapause did incur a cost in this species, in the form of prolonged preoviposition and oviposition periods, and reduced fecundity. Postdiapause conditions in their study were not different than ours, except that adults were provided with a 5% glucose solution, whereas adults in the current study were provided with a 10% glucose solution. The implication is that energy depletion during larval diapause can be compensated through adequate supplemental food intake as an adult. Therefore, the reproductive potential of *L. sticticalis* may be determined by both the amount of energy expended during diapause and energy intake after adult emergence, but further studies are needed to verify this.

The beet webworm is a long-distance migratory insect, and the flight capacity of diapause- and nondiapause-derived moths was tested on flight mills. In addition to measuring total flight duration, total distance, and mean velocity, the longest flight duration is used as the major criterion to measure flight potential of *L. sticticalis* in this study. The furthest flight distance is also considered as a secondary parameter, which is determined by both flight duration and flight velocity. Distances measured on flight mills will underestimate actual migratory flight distance in the field, because of the drag of the flight arm and absence of wind that can affect velocity greatly. Flight velocity itself, although it contributes to distance flown, may not be a good index of flight potential unless it is accompanied by long flight duration (Luo and Li 1992; Luo et al. 1995, 2002).

Results obtained in this study showed that diapause had a positive effect on the migratory flight potential of *L. sticticalis*. This may be related to increased capacity, increased propensity to engage in flight, or both. The significant increase in velocity of adults derived from diapause larvae suggests a possible increase in capacity itself. Findings of enhanced flight potential in diapause-derived individuals have been found in some other insects, such as Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Weber and Ferro 1996) and diamondback moth, *Plutella xylostella* (L.) (Shirai 1991). Although sex-related differences in flight potential have been observed in some noctuids (Sharp et al. 1975, Parker and Gatehouse 1985, Sappington and Showers 1991) and other Lepidoptera (Dorhout et al. 2008), at least at certain ages, there were no obvious differences between male and female *L. sticticalis* at 3 d of age under controlled laboratory conditions.

Unlike many other insects, the beet webworm possesses both the option to diapause and to engage in long-distance migration, which constitutes considerable life-history flexibility in distributing its offspring over space and time. Even though our results show that diapause enhances flight potential in *L. sticticalis*, we also found that long flights are not uncommon in adults with a nondiapause larval history. Furthermore, some adults with a diapause larval history did not make long flights. Thus, these two life-history strategies are not coupled in an obligate way, but both are

available to each individual as potential options. Both strategies can be used to avoid adverse conditions when environmental risks warrant. Diapause in this species represents primarily an adaptation to survive cold winters. Migration seems to be an adaptation to exploit ephemeral oviposition sites in suitable environments. In spring, the beet webworm migrates long distances from overwintering areas on the wind. The increased longevity of female adults originating from a diapause population (Jiang et al. 2010b, Fig. 1E this study) helps ensure that they have enough time for both migration and reproduction. Great flight capacity minimizes reproductive risk by making it easier to find oviposition sites and concentrate egg production in a short period just after cessation of migration.

In conclusion, the effect of diapause on postdiapause fitness, where female fecundity is traded off for survival of adverse conditions via diapause, appears to be mitigated in *L. sticticalis* by adequate energy intake by adults. Supplemental carbohydrates from nectar feeding by adults facilitates migration in the oriental armyworm, *Mythimna separata* (Walker) (Wang et al. 2006a), and may influence migratory capacity in *L. sticticalis*. The reason for enhanced migratory capacity in postdiapause adults is unclear, although it may reflect a predictable lack of suitable habitat in overwintering areas in the early spring. Although factors controlling diapause have been explored for this species (Jiang et al. 2010b), further research is needed to elucidate the factors influencing the decision to migrate, as well as the expression of migratory behavior in individuals. Finally, to close the circle and obtain a more complete picture, it will be important to determine the effects of migratory flight on fecundity and longevity.

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