

1-1-2015

Response of Reproductive Traits and Longevity of Beet Webworm to Temperature, and Implications for Migration

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Abstract

Beet webworm, *Loxostege sticticalis* (L.) is a facultative long-distance migratory insect pest in many regions between 36° and 55° N latitude. The outbreaks of larvae are closely related to temperatures encountered by the immigrant adult. But mechanisms linking population outbreaks and migration are not well understood. We investigated the effect of exposing adults to constant temperatures from 14 to 34°C on mating, oviposition, and longevity. Our results showed that both mating percentage and frequency were highest at 22–26°C and decreased at temperatures outside this optimal range. Time of night when mating began was delayed at higher temperatures, while mating duration progressively decreased with increasing temperature. Both preoviposition period (POP) and oviposition period decreased linearly with increasing temperature. Peak daily and lifetime fecundity were highest at 22–26°C and declined at temperatures outside this range, suggesting that 22–26°C is the optimal thermal range for oviposition. Adult longevity was negatively correlated with temperature. Males lived longer than females at lower temperatures, but females lived longer than males in the 30–34°C treatments. Together, our findings suggest that reproduction occurs when the prevailing temperature is around 22–26°C, and that migratory flight is favored outside this range via increases in POP and proportion of virgins. We predict that larval damage or outbreaks of *L. sticticalis* will occur only in areas where the prevailing temperature is around 22–26°C, which provides a key basis for the prediction of population outbreaks in areas of immigration.

Keywords

Loxostege sticticalis, preoviposition period, reproduction, longevity, temperature

Disciplines

Ecology and Evolutionary Biology | Entomology | Population Biology

Comments

This is an article from Cheng, Yunxia, Kai Wang, Thomas W. Sappington, Lizhi Luo, and Xingfu Jiang. "Response of reproductive traits and longevity of beet webworm to temperature, and implications for migration." *Journal of Insect Science* 15, no. 1 (2015): 154. doi: [10.1093/jisesa/iev135](https://doi.org/10.1093/jisesa/iev135). Posted with permission.

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RESEARCH

Response of Reproductive Traits and Longevity of Beet Webworm to Temperature, and Implications for Migration

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Subject Editor: Konrad Fiedler

J. Insect Sci. (2015) 15(1): 154; DOI: 10.1093/jisesa/iev135

ABSTRACT. Beet webworm, *Loxostege sticticalis* (L.) is a facultative long-distance migratory insect pest in many regions between 36° and 55° N latitude. The outbreaks of larvae are closely related to temperatures encountered by the immigrant adult. But mechanisms linking population outbreaks and migration are not well understood. We investigated the effect of exposing adults to constant temperatures from 14 to 34°C on mating, oviposition, and longevity. Our results showed that both mating percentage and frequency were highest at 22–26°C and decreased at temperatures outside this optimal range. Time of night when mating began was delayed at higher temperatures, while mating duration progressively decreased with increasing temperature. Both preoviposition period (POP) and oviposition period decreased linearly with increasing temperature. Peak daily and lifetime fecundity were highest at 22–26°C and declined at temperatures outside this range, suggesting that 22–26°C is the optimal thermal range for oviposition. Adult longevity was negatively correlated with temperature. Males lived longer than females at lower temperatures, but females lived longer than males in the 30–34°C treatments. Together, our findings suggest that reproduction occurs when the prevailing temperature is around 22–26°C, and that migratory flight is favored outside this range via increases in POP and proportion of virgins. We predict that larval damage or outbreaks of *L. sticticalis* will occur only in areas where the prevailing temperature is around 22–26°C, which provides a key basis for the prediction of population outbreaks in areas of immigration.

Key Words: *Loxostege sticticalis*, preoviposition period, reproduction, longevity, temperature

Temperature is a key factor affecting population dynamics and life history strategies of insects, because their development, survival, distribution, and abundance are directly associated with it (Parmesan et al. 1999, Bale et al. 2002). On the other hand, many insect behaviors have evolved as adaptations to thermal variation (Bale et al. 2002). For example, migration has evolved as a major life history strategy used by insects across many taxa as an adaptation to seasonal and regional temperature fluctuations (Johnson 1969, Dingle 1996). Other species physiologically escape the negative effects of extreme temperatures by entering diapause. Therefore, freeze tolerance and presence of overwintering populations have long been used as criteria to judge if a species is a true migrant. However, for some migratory species, like the oriental armyworm, *Mythimna separata* (Walker) (Li et al. 1964), black cutworm, *Agrotis ipsilon* (Hufnagel) (Showers 1997), and silver Y, *Autographa gamma* (L.) (Chapman et al. 2012), northward migration proceeds in a step-wise fashion over the summer months, involving more than one generation. In addition to helping the insects avoid the detrimental effects of high temperature on reproduction, exploiting transiently available resources may be a driving force behind this migratory strategy (Holland et al. 2006).

Reproductive traits are very sensitive to thermal variations, because both reproductive capacity and reproductive behaviors like mating and oviposition, are usually affected by temperature obviously. Although the optimum, lower and upper threshold temperatures for reproduction differ greatly among species, the time of daily mating activity is often delayed and duration of the mating window shortened as temperature increases (Showers 1997), whereas the daily peak of oviposition is less pronounced or disappears at lower temperatures (Carroll and Quiring 1993, Leather 1994). In the case of seasonal migrants, reproductive activity may not occur unless temperatures encountered by adults are optimal (Showers 1997, Huang et al. 2011). For these species, exploring variation in reproductive traits at different temperatures may provide

insights into the physiological and ecological mechanisms involved in migration, population dynamics, and pest outbreaks, phenomena which are poorly understood at present.

The beet webworm, *Loxostege sticticalis* (L.) (*Lepidoptera: Pyralidae*) is a destructive migrant insect pest of crops and fodder plants in many regions of Asia between 36° and 55° N latitude (Luo and Li 1993b, Jiang et al. 2010). As a temperate insect, its responses to thermal variation are very sensitive in affecting reproductive performance. For example, when reared from the immature to adult stage at a constant temperature in the laboratory, the greatest lifetime fecundity occurs at 22–25°C (Luo and Li 1993a). Moreover, no larval damage occurs in areas when the prevailing daily mean temperature is higher or lower than 22°C even when adults are abundant (Luo et al. 2009, Huang et al. 2011), indicating that few or no eggs are laid at such temperatures. From this, we have deduced that the thermal conditions encountered by immigrant adults are closely related to larval outbreaks in the field. It is therefore important to understand the ecological and physiological mechanisms underlying variation in reproductive performance at different temperatures encountered by adults.

Exploring these questions will improve our understanding of mechanisms underlying habitat selection by adults, population dynamics, and development of efficient forecasting and management strategies. Furthermore, temperatures in the home range of *L. sticticalis* have risen 1–2°C from 1970 to 2004, due to global warming (IPCC 2007), and the effects of continued change on where damage can be expected is an important new question. Based on the above considerations, we report the effects of constant temperature during the adult stage on mating oviposition, and longevity of adult *L. sticticalis*. The implications of the results are discussed relative to field investigations of migration, population dynamics, reproduction, and larval outbreaks. Possibilities for establishing technologies for forecasting and management of *L. sticticalis* are also discussed.

Materials and Methods

Colony maintenance. A laboratory colony of *L. sticticalis* was established with diapausing larvae collected from the field in Kangbao county (114. 63° E, 41. 87° N) of Hebei province, China, in 2012. The colony had been maintained for three generations when the experiments began. Larvae, pupae, and adults were maintained at room temperature and a photoperiod of 16:8 (L:D) h. Adults emerging on the same day were collected and held together in a 2-liter plastic cage (self-made) for mating and oviposition. Adults were provided daily with 10% glucose solution (w/v). Eggs laid on gauze were collected daily and transferred to another plastic cage. After hatching, larvae were transferred to a transparent glass jar (850 ml, self-made) and fed daily with fresh leaves of lambsquarters, *Chenopodium album* (L.). When larvae stopped feeding, sterilized soil (10% moisture content) was added to the cages to a depth of 10 cm to provide a substrate for cocoon formation, pupation, and adult emergence.

Test insects. Newly hatched larvae were reared at a density of 30 larvae per 850-ml glass jar. The number of larvae was maintained at constant density throughout the feeding period. Excess food was provided by adding fresh leaves of *C. album* each morning. All stages of the tested insects were maintained at a constant temperature of 22°C, 70% RH, and photoperiod of 16:8 (L:D) h. These conditions inhibited diapause and ensured maximum survival, development rate, and reproductive capacity (Luo and Li 1993a).

Treatments. Newly emerged adults were individually paired in a plastic cylinder (8 by 20 cm) and provided with 10% glucose solution (w/v), which was changed daily. They were maintained in an environmental chamber (Ningbo, China) at temperatures of 14, 18, 22, 26, 30, or 34°C. These temperatures represent the range of temperatures adults may encounter in the field during the breeding season. Other environmental conditions were the same as those used for colony maintenance. Twenty-five pairs of adults were used for each treatment. The realized sample size was sometimes <25 because moths that escaped or died before mating were excluded.

Mating activities. Mating of *L. sticticalis* occurs only during the scotophase (Wang et al. 2011). Mating activity under the different temperature treatments was observed during the scotophase beginning the day when the experiments were set up. Observations were made at 15-min intervals using a red flashlight. Time of initiation and duration of copulation for each mating event were recorded. The female was dissected after death to confirm mating success based on presence of a spermatophore in the spermatheca.

Oviposition parameters and lifetime fecundity. The preoviposition period (POP), oviposition period, and lifetime fecundity were measured under the different temperature treatments. POP was measured as the period from the day of emergence to the day when oviposition began. The oviposition period covered the period from the first to the last day of oviposition. The number of eggs laid was counted and recorded daily throughout life. The day on which the greatest number of eggs was counted during the oviposition period constituted the day of peak fecundity. The total number of eggs laid by a female constituted lifetime fecundity. All parameters were derived only from mated females.

Adult longevity. The longevity of the adults was counted from the day of emergence to the day of death. Survival of the male and female was checked daily.

Data analysis. All numeric values obtained from the studies are presented as mean \pm SE. All data were checked for normal distribution with the Kolmogorov–Smirnov test. Differences between treatments were evaluated by one-way analysis of variance. Significant differences among multiple means were determined by Tukey's Honestly Significant Difference (HSD) test. Differences in longevity between the genders were evaluated by Student's *t*-tests. Mating percentage was analyzed by a chi-square test. Relationships between longevity and temperature were evaluated by linear regression analyses. All statistical procedures were performed with SPSS 16.0.

Results

Mating capacity and activity. Mating percentage was significantly affected by temperature ($\chi^2 = 33.01$, $df = 5$, $P < 0.0001$) (Fig. 1A). Almost all moths mated at 22 and 26°C with significantly fewer mating in the other temperature treatments ($P \leq 0.011$). No significant differences in mating percentage were found between the 22 and 26°C, the 30, 14, and 18°C, or the 14 and 34°C treatments ($P \geq 0.29$). Mating percentage at 34°C was significantly lower than those at other temperatures ($P \leq 0.025$) except 14°C.

Temperature had a significant effect on number of lifetime matings ($F_{5, 132} = 11.88$, $P < 0.0001$) (Fig. 1B). Moths in the 22 and 26°C treatments mated an average of 2.4 and 2.2 times, respectively, and did not differ significantly ($P = 0.99$), but were significantly greater than those at 14, 18, and 34°C ($P \leq 0.04$). Moths in the 18 and 30°C treatments mated only 1.2 times on average. Moths at the lowest (14°C) and highest (34°C) temperatures often did not mate at all.

Mating activity began in the second half of the scotophase, and was significantly affected by temperature ($F_{5, 163} = 34.23$, $P < 0.0001$) (Fig. 2A). Mating initiation at 14 and 18°C was significantly different ($P = 0.04$), and both were significantly earlier than at the four higher temperatures ($P < 0.0001$). The initiation time of mating at 22°C was significantly earlier than that at 34°C ($P = 0.007$). Time of mating initiation at the four higher temperatures did not differ significantly ($P \geq 0.13$).

Mating duration ranged from 19 to 124 min and was significantly affected by temperature ($F_{5, 163} = 22.61$, $P < 0.0001$; Fig. 2B). It lasted as long as 84.5 min at 14°C, and decreased with increasing temperature to only 34.7 min at 34°C ($P < 0.0001$), half that at 14°C. Mating duration at 14 and 18°C did not differ ($P = 0.97$), but lasted significantly longer than in the other four treatments ($P \leq 0.03$). Mating duration at 22°C did not differ from that at 26°C ($P = 0.65$), but was significantly greater than at 30 and 34°C ($P \leq 0.01$). Mating duration at 26°C did not differ from that at 30°C ($P = 0.65$), but was significantly longer than at 34°C ($P = 0.006$). Mating duration did not differ significantly at 30 and 34°C ($P = 0.46$).

Oviposition behavior and fecundity. POP was significantly affected by temperature ($F_{5, 111} = 141.10$, $P < 0.0001$), being longer at lower temperatures than high (Table 1). The greatest POP (22 d) was observed at 14°C and differed significantly from that in the other treatments ($P < 0.0001$). The POP at 18°C lasted 13 d and was significantly longer than that at higher temperatures ($P < 0.0001$). POP in the treatments of 22, 26, and 30°C did not differ significantly ($P \geq 0.05$), but was significantly longer at 22°C than that at 34°C ($P \leq 0.008$).

Oviposition period was also significantly affected by temperature ($F_{5, 111} = 33.21$, $P < 0.0001$), declining with increasing temperature (Table 1). Moths at the four lower temperature treatments oviposited for significantly more days (> 10) than those at the two higher temperatures (< 8).

Daily number of eggs oviposited usually peaked on the second or third day after onset of oviposition (Fig. 3), after which daily egg production declined. The temporal pattern of oviposition and number of eggs laid was affected by temperature ($F_{5, 111} = 20.30$, $P < 0.0001$) (Fig. 3). Peak daily fecundity at 22°C was significantly greater than at 14, 18, and 34°C ($P \leq 0.003$), but was not significantly different from that at 26 and 30°C ($P \geq 0.13$).

Lifetime fecundity was significantly affected by ambient temperature ($F_{5, 111} = 140.92$, $P < 0.0001$). The moths at 22 and 26°C oviposited significantly more eggs than the moths at any other treatments did ($P < 0.0001$). Lifetime fecundity did not differ between 22 and 26°C ($P > 0.05$), or between 18 and 30°C ($P > 0.30$), but that at 14 and 34°C differed significantly from that at 18 and 30°C ($P < 0.0001$).

Longevity of both genders. Longevity of both male and female adults was negatively correlated with ambient temperature, but the response differed by sex (Fig. 4) (for females, $Y = -1.12X + 51.76$, $r^2 = 0.95$, $P < 0.0001$; for males, $Y = -1.75X + 68.11$, $r^2 = 0.98$, $P < 0.0001$). Males lived longer than females at 14 ($t = -2.56$, $df = 32$,

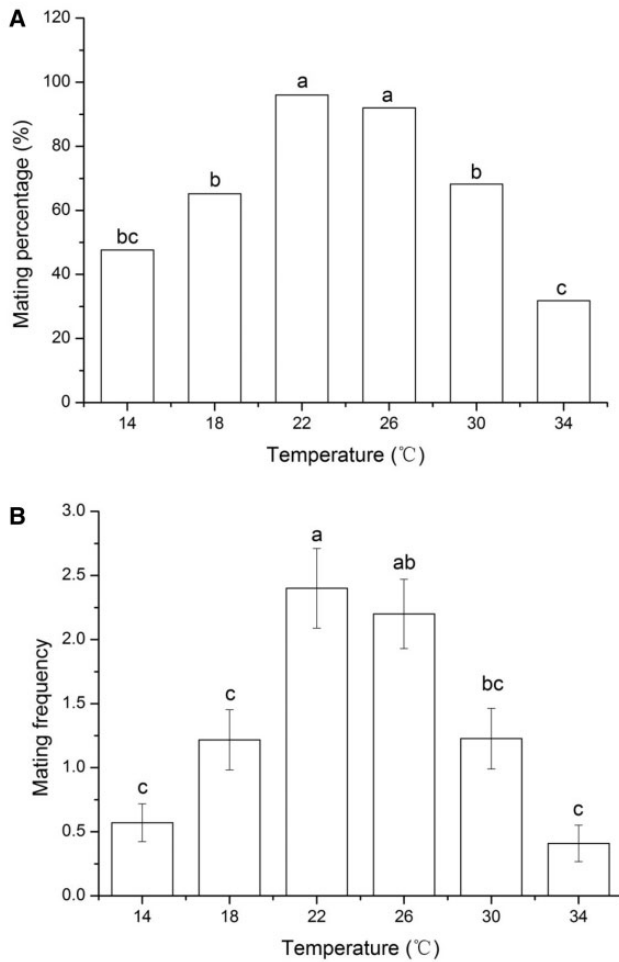


Fig. 1. The effect of temperature in adult stage on mating percentage (A) and frequency (B) in *L. sticticalis*. Bars sharing the same letter are not significantly different in each panel. Sample sizes from left to right (A and B) are 21, 23, 25, 25, 22, and 22, respectively.

$P = 0.02$) and 22°C ($t = -5.04$, $df = 29$, $P = 0.0001$), but shorter than females from 30 ($t = 2.89$, $df = 34$, $P = 0.007$) to 34°C ($t = 3.41$, $df = 38$, $P = 0.002$). Longevity between the genders did not differ significantly at 18 ($t = -1.59$, $df = 28$, $P = 0.12$) and 26°C ($t = -1.32$, $df = 44$, $P = 0.19$).

Discussion

Mating behavior and percentage. Mating behavior of *L. sticticalis* differed significantly under different thermal conditions (Figs. 1 and 2). The time at which mating activity began at night was delayed as temperature increased within the range of 14–34°C. This result is consistent with those obtained from other Lepidoptera, including *Trichoplusia ni* (Hübner) (Sower et al. 1971), *Argyrotaenia velutinana* (Walker), *Virbia immaculata* (Reakirt) (Carde et al. 1975), and *Spodoptera exigua* (Hübner) (Wang et al. 2004) tested under different temperature regimes. Variation in timing of daily mating activity may result from the effects of temperature on the release of female sex pheromone and the response of males (Sower et al. 1971, Dong and Du 2002). In contrast, mating duration of *L. sticticalis* decreased linearly as temperature increased. This result is consistent with findings for *S. exigua* (Wang et al. 2004), and the beetle *Callosobruchus chinensis* (L.) (Katsuki and Miyatake 2009). In *C. chinensis*, there is a negative relationship between ambient temperature and mating duration, sperm transfer and sperm transfer duration (Katsuki and Miyatake 2009). In *L. sticticalis*, mating duration is linearly extended as the moths age (Wang et al. 2011). We suspect

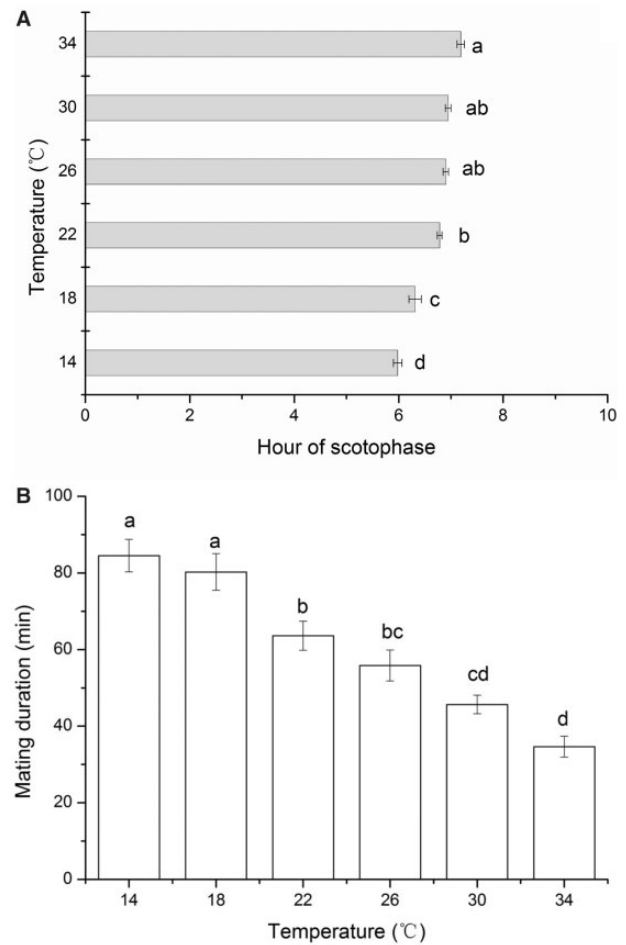


Fig. 2. The effect of temperature in adult stage on initiation time (A) and duration (B) of mating in *L. sticticalis*. Bars sharing the same letter are not significantly different. Sample sizes, from top to bottom (A) and left to right (B), are 32, 26, 34, 31, 26, and 20, respectively.

that the earlier incidence of daily mating activity at lower temperature is an adaptive behavior to guarantee completion of the mating process within the scotophase since the mating activities last longer, and are completely terminated by dawn.

Our results also showed that mating success (percentage and frequency) of *L. sticticalis* was greater from 22 to 26°C, indicating this is the optimal temperature range for mating. This is consistent with results obtained in other moth species, which exhibit a range of suitable temperatures for mating, outside of which success declines (Simmons and Marti 1992, Wang et al. 2004). This is also supported by evidence from the field that the proportion of virgin males and females increased sharply when daily mean temperature was greater or less than 22°C (Luo et al. 2009). Reasons for the lower mating success outside of 22–26°C are not completely understood. Refusal of females to mate at temperatures below 22°C may be adaptive, given that mating duration at these temperatures is remarkably extended and may injure the female (Katsuki and Miyatake 2009). Lower mating success at higher temperatures may result from increasing failure to couple. For example, *L. sticticalis* males exposed to 35°C were unable to couple with untreated females to a normal extent (Tribel and Kolmaz 1981). *Agrotis infusa* (Boisduval) males became sterile, and copulation often failed to occur, or was abnormal, when the moths were kept at 30°C (Rewat 1971). *M. separata* moths are completely unable to mate at 33°C (Jiang et al. 2000). These findings suggest that temperature is a major factor determining the mating success of insect.

Table 1. Mean (\pm SE) preoviposition period, oviposition period, peak daily, and lifetime fecundity of *L. sticticalis* exposing adult at different constant temperatures

Temperature ($^{\circ}$ C)	N	POP (d)	Oviposition period (d)	Peak daily fecundity	Lifetime fecundity
14	17	22.41 \pm 0.66a	13.00 \pm 0.39a	38.24 \pm 1.41d	147.82 \pm 7.76c
18	15	13.33 \pm 0.54b	11.67 \pm 0.64ab	58.07 \pm 2.64bc	197.40 \pm 8.12b
22	24	7.58 \pm 0.36c	10.29 \pm 0.56b	76.46 \pm 4.01a	327.25 \pm 7.93a
26	23	7.13 \pm 0.36cd	10.35 \pm 0.47b	72.13 \pm 4.08ab	298.70 \pm 6.88a
30	18	5.94 \pm 0.32cd	7.83 \pm 0.54c	65.00 \pm 3.2abc	222.28 \pm 8.40b
34	20	5.20 \pm 0.19d	4.95 \pm 0.18d	47.35 \pm 1.72cd	115.55 \pm 3.26d

Means in a column sharing the same letter are not significantly different.

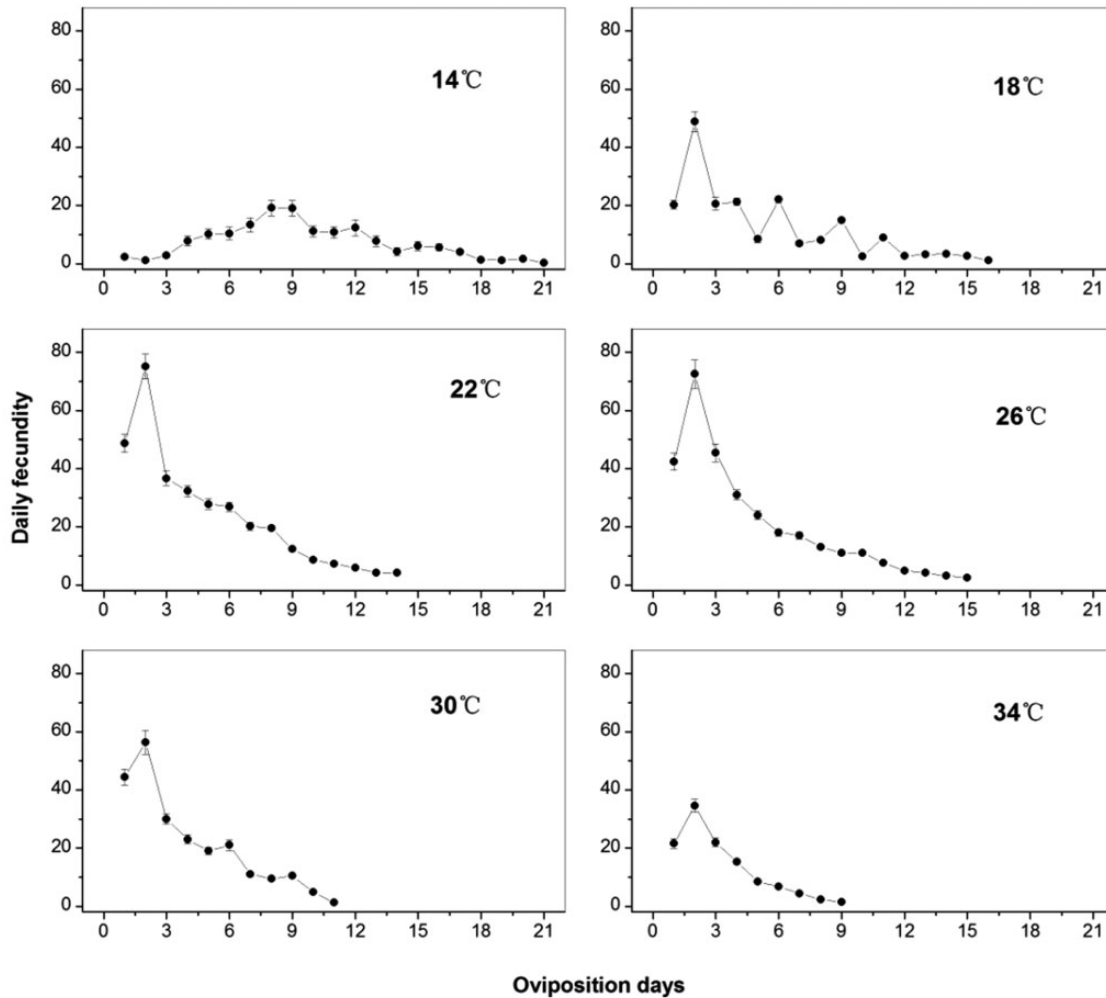


Fig. 3. Number of eggs laid daily by *L. sticticalis* exposing adult at different temperatures. Sample sizes, from low to high temperature treatment, are 17, 15, 24, 23, 18, and 20, respectively.

An implication of our findings is that the proportion of virgin moths will be increased when ambient temperatures fall outside the 22–26 $^{\circ}$ C range, which will favor the migration of the moths (Cheng et al. 2013).

Oviposition pattern and life time fecundity. Our results show that the POP of adult *L. sticticalis* decreases linearly with increasing temperature (Table 1), a pattern consistent with those observed in the moths *Panolis flammea* (Denis and Schiffmuller) (Leather 1994), and *S. exigua* (Wang et al. 2004). However, the effects may be variable at higher temperatures. For example, POP in *L. sticticalis* was significantly prolonged at 34 $^{\circ}$ C than at 22–30 $^{\circ}$ C (Luo and Li 1993a). In addition, sexual maturation of males may also be affected by temperature, which in turn would affect age of copulation and, thus, POP within a cohort. Because

L. sticticalis moths with long POP usually have great flight potential and a longer time window to engage in migration (Kong et al. 2010), temperature may serve not only as an important environmental cue affecting reproductive activity, but also as a major promoter of migration through its physiological effects on development.

Temporal patterns of oviposition activity by *L. sticticalis* differ under different temperature regimes (Fig. 3). Oviposition patterns at temperatures lower than 22 $^{\circ}$ C are generally flatter than those \geq 22 $^{\circ}$ C, which is consistent with those in other moth species (Carroll and Quiring 1993, Leather 1994). The numerical peak of daily oviposition at 22 $^{\circ}$ C is also consistent with the results of Luo and Li (1993a) for *L. sticticalis*. In several other moth species, peak daily fecundity was also greater at the optimum temperature for lifetime fecundity than at other

temperature treatments (Carroll and Quiring 1993, Leather 1994, Wang et al. 2004). For example, the peak of daily fecundity in *Zeiraphera canadensis* (Mutuura and Freeman) at 20°C was far greater and more distinct than at 10°C, the lowest temperature tested (Carroll and Quiring 1993). Given that the oviposition period of *L. sticticalis* does not differ significantly from 14 to 26°C, peak daily fecundity may be a better indicator of the optimum temperature for oviposition. A sharp peak in fecundity at 22–30°C suggests that an outbreak population is easier to form in fields experiencing temperatures in this range.

We found that lifetime fecundity of *L. sticticalis* is maximum at 22–26°C, but declines when temperature is outside that range, which is consistent with a previous study that tested rearing temperatures at all life stages ranging from 16 to 34°C (Luo and Li 1993a). Field studies indicate that larval outbreaks always occur when daily temperatures

average around 22°C (Luo et al. 2009, Huang et al. 2011), indicating that reproduction is most successful under these thermal conditions. Outbreak populations at the daily mean temperatures around 22°C thus seem to result from the combined effects of greatest lifetime fecundity from 22 to 26°C and peak daily fecundity at 22–30°C.

We suspect that mating success is the major proximate cause of variation in lifetime fecundity because both mating success and lifetime fecundity are greatest at 22–26°C. Mating often serves not only as a stimulant for oviposition, but male contributions can provide additional nutrient resources for egg formation and development, as demonstrated in other moths (Proshold et al. 1982, Park et al. 1998).

Adult longevity. Adult longevity of moth species generally decreases as temperature increases (Henneberry and Clayton 1991, Leather 1994, Jiang et al. 2000), and both sexes of *L. sticticalis* showed the same trend within the range of 14–34°C. However, the effect of temperature on male longevity, which is seldom examined in other studies, differed greatly from that of the females (Fig. 4). Males lived longer than females at temperatures below 26°C but shorter than females at 30 and 34°C, consistent with the results of Luo and Li (1993a). These results suggest that males are more sensitive to high temperatures than females. The decline in adult longevity, particularly in males at the higher temperature may contribute to the poor reproductive performance of *L. sticticalis* at elevated temperatures. In other moths, poor reproductive performance at the upper threshold temperature is generally correlated with a reduction in adult longevity (Carroll and Quiring 1993, Leather 1994, Wang et al. 2004). Escaping the detrimental effects of temperature on reproduction and longevity may be a priority for adults emerging in an area of high temperature. Migration is a way to extend adult longevity and reach the maximum reproductive potential in *L. sticticalis*.

Implications. Reproductive performance was best at 22–26°C among the temperatures tested from 14 to 34°C, and we conclude that 22–26°C is the optimal range of temperatures for reproduction in *L. sticticalis*. *L. sticticalis* is a facultative long-distance migrant that migrates prereproductively (Feng et al. 2004, Chen et al. 2012), and moths with a long POP have great flight capacity (Kong et al. 2010). We expect that migratory flight is activated in areas where temperatures fall outside the range of 22–26°C, because the POPs are extended (Table 1) and proportions of virgins are increased (Fig. 2). We summarized our conclusion graphically (Fig. 5) and it is also supported by radar observations that migratory flight activity is enhanced at 17–20°C

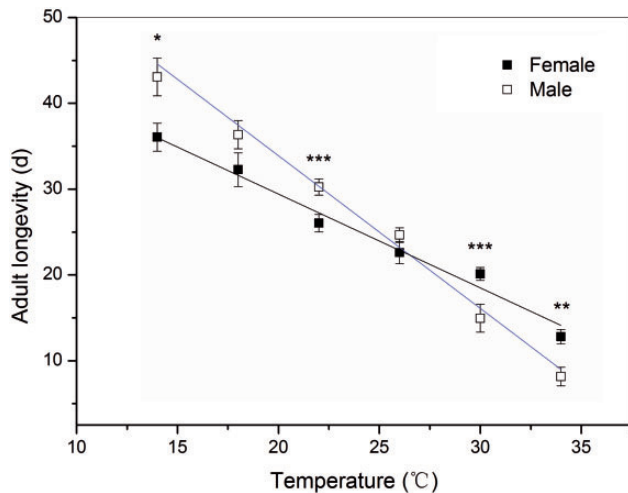


Fig. 4. Relationship between the longevity of adult female and male *L. sticticalis* maintained at different temperatures. One, two, or three asterisk (s) indicate that the difference between the genders at the given temperature is significant at $P < 0.05$, $P < 0.01$, and $P < 0.01$, respectively, as determined by Student's *t*-tests. Sample sizes for both females and males, from the left to right, are 17, 15, 24, 23, 18, and 20, respectively.

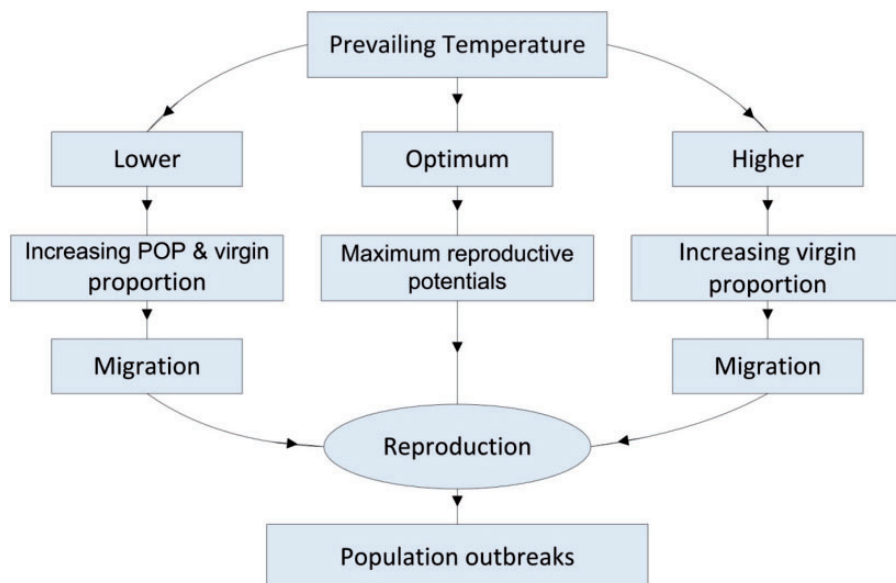


Fig. 5. Schematic illustration of the relationship between reproduction, migration, and larval outbreaks of *L. sticticalis*, as affected by prevailing temperatures when adult populations are abundant.

(Feng et al. 2004), as is that of adults which develop from larvae or pupae experiencing high temperature. However, to date there is no direct field evidence that migratory flight activity is triggered by daily mean temperatures $>26^{\circ}\text{C}$.

Migration continues when *L. sticticalis* land at a site where the daily mean temperature is lower than 22°C (Cheng et al. 2013). Thus, migrating to an area with optimal thermal conditions ($22\text{--}26^{\circ}\text{C}$) to reproduce may be the first mission of adult *L. sticticalis* emerging at temperatures outside of that optimal range, as in other migrant insect species (Holland et al. 2006). This conceptual model of facultative migration may help explain the stepwise northward migration phenomenon observed in other seasonal migrants (Li et al. 1964, Showers 1997, Chapman et al. 2012).

Our results demonstrate that all measured reproductive traits of adult *L. sticticalis* are optimal at $22\text{--}26^{\circ}\text{C}$, which is consistent with field observations that all larval damage, either in spring (May to June) or fall (August to September) (Luo et al. 2009, Huang et al. 2011) occur in areas where the daily mean prevailing temperature is around 22°C . This suggests that adult seeks to oviposit only under optimum thermal conditions, although humidity is also critical for reproduction of *L. sticticalis*. Thus, we predict that larval outbreaks or damage will occur only in areas where the prevailing daily mean temperature is around $22\text{--}26^{\circ}\text{C}$ receiving an influx of adult migrants. The possibility of outbreaks in these areas will be enhanced by the synchrony of oviposition promoted by migratory flight (Cheng et al. 2012). We further hypothesize that the incidence of larval damage may extend spatially in the future to higher altitudes and latitudes than at present, propelled by global warming, which is predicted to be especially prominent in the current range of *L. sticticalis*.

Acknowledgments

This work was financially supported by National Natural Science Foundation of China (No: 31301656; 31371947), Special Fund for Agro-Scientific Research in the Public Interest (201303057; 201403031), and International Science & Technology Cooperation Program of China (2014DFR31250).

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Received 11 September 2015; accepted 7 October 2015.