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Growth, development and daily change in body weight of *Locusta migratoria manilensis* (Orthoptera: Acrididae) nymphs at different temperatures

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Abstract

We reared Oriental Migratory Locusts, *Locusta migratoria manilensis* (Meyen) in the laboratory from 3rd instar until adult death, at five constant temperatures (18, 21, 24, 27 and 30°C), and recorded life history variables. Temperature strongly influenced growth, development and behaviors. Growth and development rates were both positive linear functions of temperature, with low thermal thresholds for nymphal growth (15°C) and development (13°C). There was no mating at 18°C and no oviposition at 21°C and below. Rearing temperature did not significantly influence mass at adult molt, except for the 18°C-nymphs who molted to adults with significantly smaller mass. Females laid their first egg pod significantly later at 24°C than at 30°C. There were strong but nonsignificant trends for low-temperature females to die earlier and lay fewer and lighter egg pods; 24°C-females averaged less than half the dry lifetime egg mass as 30°C-females. Our results show that *L. m. manilensis* is a warm-climate species, and explain its current range and phenology in China. Knowledge of the thermal physiology and thermal ecology of *L. m. manilensis* will aid in its control and in predicting future outbreaks.

Key words

temperature, growth, mass, development, life history, oviposition, mating, longevity, China

Introduction

Temperature is of vital importance to insects because they are exothermic. As such, their body temperatures mirror environmental temperatures and thus are constantly changing (May 1985; Zhang 2002). This is a problem for insects, because most biological processes vary with temperature (Zhang 2002; de Jong & van der Have 2009). This is particularly true for grasshoppers, where behavior, metabolism, growth, development, life-history, population dynamics and geographic range are all strongly influenced by temperature (Chappell & Whitman 1990; Willott & Hassall 1998; Fielding 2004). For example, behavior requires muscle action, which declines rapidly at low temperatures (Josephson 1981; Wang & Chen 1989). In grasshoppers, rates of feeding, walking, flying, dispersal, molting, mating and oviposition are reduced at low temperatures, and cease altogether at cold temperatures (Whitman 1988; Chappell & Whitman 1990; Lactin & Johnson 1995, 1996).

Growth (= mass gain) is also thermal dependent because growth depends on rates of energy gain, which are determined by feeding, digestion, assimilation and metabolic rates, all of which correlate strongly with temperature (Whitman 1988; Yang & Joern 1994; Harrison & Fewell 1995). As temperatures decline, growth rates decline, until eventually the low-temperature threshold for growth is reached, at which point no growth is possible.

Development is also controlled by temperature, and within suitable thermal limits grasshoppers generally develop faster at higher temperatures (Whitman 1986; de Jong & van der Have 2009). For example, in *Melanoplus sanguinipes* (Fabricius) from Alaska, nymphal development requires 65 d at 21°C, but only 16 d at 39°C (Fielding 2004). Temperature can also determine the number of times an individual molts, which alters both time-to-adult and adult body size (Willott & Hassall 1998; Lactin & Johnson 1998a; Maeno & Tanaka 2010). As temperatures decline, grasshopper development rate usually slows, until the low thermal threshold for development is reached, at which point no development takes place (Rodríguez-Absi *et al.* 2009). Interestingly, the low-threshold points for growth and development are often at different temperatures. In such cases, a body temperature intermediate between the two thresholds allows one process to continue, but not the other, depending on which threshold (growth or development) is lower (Lactin & Johnson 1998a, 1998b). Differences between relative growth and development rates at different temperatures explain why adult body size depends on rearing temperature (Whitman 1986; Lactin & Johnson 1998a, 1998b; Whitman 2008; Blanckenhorn 2009).

Different grasshopper species have evolved different physiological adaptations to temperature. Some species are cold adapted and survive well in cool habitats (Zhang 2002; Walters & Hassall 2006; Finch *et al.* 2008). Other species are warm-adapted (Zhang 2002). These physiological/genetic adaptations help explain the geographic distributions of different grasshopper species. For example, *Chorthippus dubius* (Zubovskii) from Inner Mongolia develops fastest at 30°C (Wang *et al.* 1988), whereas *Locusta migratoria migratorioides* (Reiche & Fairmaire) from Africa develops fastest at 42°C (Hamilton 1950). Likewise, it is reported that *Gomphocerippus brevipennis* from the Pyrenees Mountains can walk at temperatures as low as 5°C (Marty 1961), whereas *Sphingoderus carinatus* from the Egyptian desert can only walk at temperatures above 24°C (Hafez & Ibrahim 1965). Although Uvarov (1977) cautions that these specific values (*i.e.*, 5 vs 24°C) were derived using different methods, the fact remains that grasshopper species clearly differ in thermal physiology (*e.g.*, see Table 5 in Uvarov 1977).

Because temperature strongly influences their biology, grasshoppers have evolved mechanisms to regulate their temperature (Chappell & Whitman 1990; Lactin & Johnson 1996; Miller *et al.* 2009). On cold days, grasshoppers heat by basking in the sun or hugging warm substrates (Lactin & Johnson 1996; Miller *et al.* 2009). On excessively hot days, grasshoppers move off the ground into shade and some even cool via evaporation (Lactin & Johnson 1996; Miller *et al.* 2009). On sunny days, grasshoppers can compensate

for cold air temperature by heating their bodies via solar basking (Lactin & Johnson 1996; Miller *et al.* 2009), and thus continue to grow, develop, and perform behaviors, even when air temperatures are below the threshold for these activities (Chappell & Whitman 1990).

The relationships of grasshoppers to temperature are complex (Uvarov 1966, 1977; Chappell & Whitman 1990; de Jong & van der Have 2009). For example, the effect of temperature may change over time (Whitman 2009) and among instars, populations, and species (Whitman 1987; Lactin & Johnson 1995; Telfer & Hassall 1999), and are difficult to interpret (Shi & Ge 2010). Most important, however, is that climate, and especially temperature, can determine grasshopper survival, geographic distribution, reproductive success, and population dynamics (Whitman 1988; Joern & Gaines 1990; Guo *et al.* 1991). That is why cold, rainy weather tends to decrease grasshopper populations even when food is abundant (Guo *et al.* 1991; Powell *et al.* 2007). Cold slows feeding, growth and development, and clouds prevent heating via solar basking (Chappell & Whitman 1990; Stauffer & Whitman 1997). In contrast, dry, hot weather generally increases grasshopper populations, as long as there is suitable food (Joern & Gaines 1990; Guo *et al.* 1991). Under warm, dry conditions, grasshopper populations can grow rapidly to become an agricultural/economic problem (Ma 1958).

In order to monitor, predict, and control grasshopper pests, it is essential to understand how temperature influences grasshopper biology (Brust *et al.* 2009). In this paper, we investigate the thermal biology of the Oriental Migratory Locust, *Locusta migratoria manilensis* (Meyen) (Orthoptera: Acrididae), one of 10 migratory locust subspecies (Uvarov 1977; Kang *et al.* 1989; Chen 1991; Zhang *et al.* 2003, 2009). *L. m. manilensis* is thought to breed in China, the Philippines, and possibly Viet Nam. From these breeding zones, they are thought to make swarming flights into Cambodia, Laos, Thailand, Indonesia, Borneo, and Malaysia (Uvarov 1977; Chen 1991). In China, this locust completes 1 to 4 generations per year, depending on latitude and weather (Chen 1991; Zhu 1999). It is widely distributed at latitudes near 42°N in China, where there is one generation per year (Zhu 1999; Chen 1991, 2000). As with other *L. migratoria* subspecies, *L. m. manilensis* can undergo phase transformation, and hence exist in a solitary or gregarious phase. It overwinters in the egg stage, but lacks an obligate egg diapause (Chen 1991). The low-temperature threshold for egg development is thought to be ~ 15°C, and for hatching, 16°C (Chen 1991). Temperatures between 20°C and 42°C are suitable for nymphal development (Chen 1991). In different studies, females have averaged from 2 to 7 pods, and 44 to 99.5 eggs per pod, and one female laid 12 pods (Chen 1991).

Throughout its range, *L. m. manilensis* can be a major pest of cereal crops, causing economic loss (Chen 1979, 2000, 2007; Chin 1985; Zhu 1999). It has long been known that this pest is cyclical and that such cycles were related to the weather (Ma 1958). In fact, Chinese farmers have a saying: "floods, droughts and locust plague as a family", because historically, locust plagues have appeared after flood & drought (Chen 2007).

In this study, we investigated how temperature influences the life history traits of *L. m. manilensis*. We mainly examined lower, suboptimum temperatures, which locusts are normally exposed to in the field. Such temperatures might limit their growth, development, behavior, body size, survival and reproductive capacity, and thus influence their population numbers and pest status (Zhu 1999). This information will help us understand locust population dynamics, help us model and predict their life history and phenology in the field, and facilitate locust control. In addition, understanding the

thermal relationships of locusts will aid maintenance of laboratory colonies, upon which laboratory research on alternative control methods, such as toxicology and pathology depends.

Materials and Methods

Study organism.—We studied the Oriental Migratory Locust, *Locusta migratoria manilensis* (Meyen). Eggs were collected in November (Autumn locust) from the field in Cangzhou City, HeBei Province, China, and brought to the Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing.

Rearing methods and experimental conditions.—Locust eggs were transferred to growth cabinets (PRX-350B-30) maintained at 27 ± 0.5°C, 60 ± 5% RH, and 12:12 L:D photoperiod (Wang *et al.* 1988). Resulting hatchlings were maintained in communal cages under these same conditions until the 3rd instar.

Effect of rearing temperature on nymphal development rate, growth rate, and maximum pre-adult mass.—Fifty newly molted 3rd instar nymphs were removed from hatching cages and divided randomly into five groups of 10 individuals. Each group was assigned to one of five temperature treatments (18, 21, 24, 27 and 30°C), and thereafter maintained in environmental chambers under 12:12 L:D photoperiod and constant temperature. Each insect was held individually in an unventilated 500-ml clear plastic container with a snap-on plastic lid, fed twice a day with fresh-cut wheat leaves (*Triticum sativa* L.), and once a day with artificial diet (100 g wheat bran + 5 ml corn oil + vitamin B & C). All 50 individuals were weighed daily to the nearest 0.1 mg, using an electronic balance. Each treatment contained males and females, and continued from the beginning of the 3rd instar to the adult molt. A few individuals died before maturity, but were immediately replaced by reserve individuals that had been maintained under identical conditions.

Effect of temperature on development of adults.—Ten freshly molted adults (5 ♂, 5 ♀) were obtained from nymphs reared at each of five temperatures (18, 21, 24, 27 and 30°C), and thereafter maintained in incubators at the same constant temperature and conditions as before. Adults were confined in pairs (1 ♂ + 1 ♀) in clear 500-ml plastic containers at each temperature (five pairs/temperature). For each adult female, we recorded the premating interval, oviposition timing, pre- and postoviposition masses, number of clutches laid, dry mass of eggs laid, and adult longevity. The containers lacked sand, so females laid pods on the floor or sides of the containers. The resulting egg mass was collected, dried at 80°C in an oven for 24 h, and then weighed on an electronic balance to the nearest mg.

Data analysis.—Nymphal growth rate was calculated from the change in fresh body mass between molts. Maximum body weight of each nymph and developmental parameters of adults were estimated using SAS (Statistic Analysis System) and simple regression statistics. The slopes and characteristics of growth curves were compared for each instar at different temperatures (Kingsolver *et al.* 2006).

Results

Daily growth of nymphs at five different temperatures.—Figure 1 plots the daily mean masses of *L. m. manilensis* nymphs reared at five different constant temperatures. Nymphs gained mass daily, except at the time of molting, at which time they generally lost weight. Hence, maximum mass for each instar was at about one or two days prior

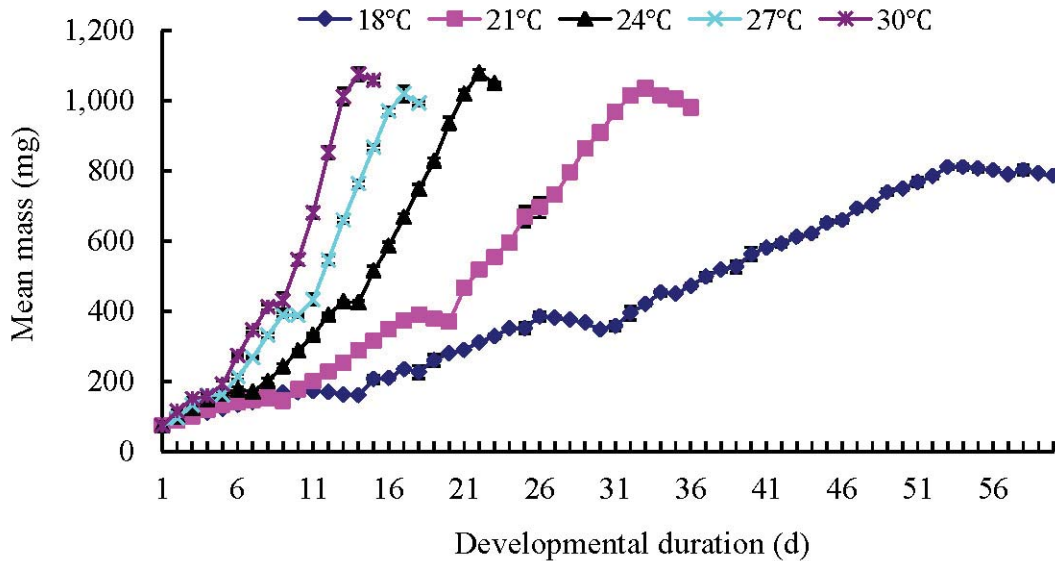


Fig. 1. Daily live body weights of *L. m. manilensis* 3rd to 5th-instar nymphs at different temperatures. Each growth line represents the mean of the same 10 mixed-sex individuals maintained at constant temperature and weighed daily from the beginning of the 3rd to the end of the 5th instar. Points where the growth lines level off or decline represent molting events.

to the molt. This decline in mass at molting is most clearly seen at the end of the 5th instar for all five temperatures (Fig. 1).

Figure 1 also shows that absolute mass gain/d is a function of instar number, body size, and temperature. Thus, at 30°C, the small 3rd instars added ~27 mg/d, whereas the larger 5th instar nymphs add ~95 mg/day (Fig. 1). For each of the highest four temperatures, ~62 % of total nymphal mass was acquired during the 5th (last) nymphal instar (Fig. 2). There was no significant difference in maximum weights of 3rd-instar ($F=0.24$, $n=39$, $P>0.05$) and 4th-instar ($F=0.40$,

$n=48$, $P>0.05$) nymphs raised at the five different temperatures, as determined by ANOVA and Duncan's multiple-range test (Fig. 2). In the case of 5th instar nymphs, there were no significant differences in maximum weights of nymphs kept at 21, 24, 27 and 30°C ($F=0.06$, $n=47$, $P>0.05$), but the maximum weights of these nymphs were significantly higher than nymphs kept at 18°C (Fig. 2).

Nymphal growth rates.—Nymphs grew faster when reared at higher temperatures (Fig. 1) and this was true for all instars and temperatures

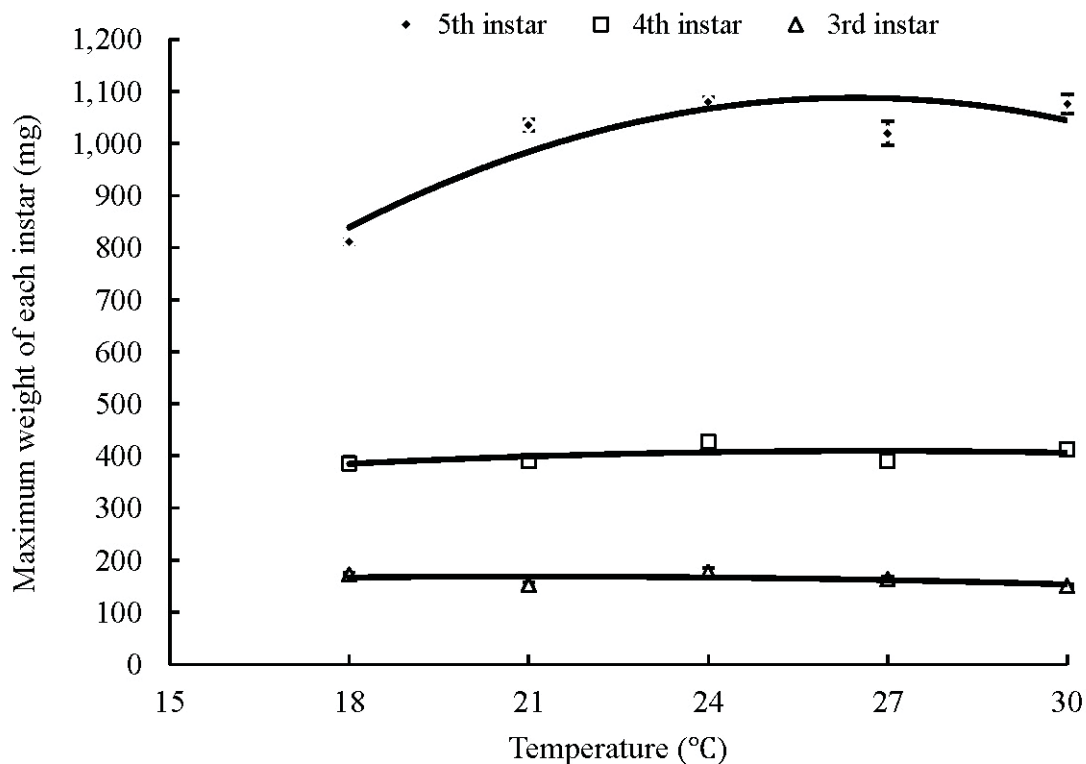


Fig. 2. Mean maximum live body weight achieved by nymphs at different instars and temperatures. Ten individual mixed-sex nymphs maintained and measured at each rearing temperature.

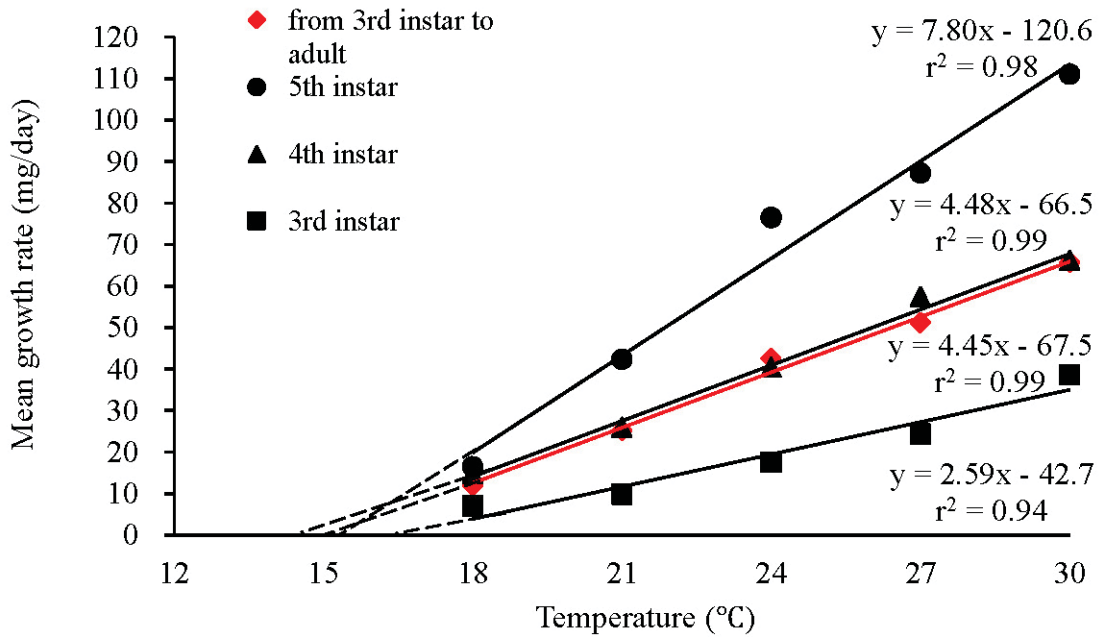


Fig. 3. Relationship between temperature and nymphal growth rate. Solid lines show regressions based on empirical data. Dashed lines show theoretical extension of regression lines to x-axis. The points where the lines intersect the x-axis represent the Theoretical Low Temperature Threshold for Growth.

tested (Fig. 3). For each instar, growth rate was a linear function of temperature (Fig. 3). Extending these growth rate vs temperature regression lines to the x-axis gives us the theoretical low temperature threshold for growth. Note that these values converge to ~15°C for the 4th, 5th, and total (3rd-to-adult molt) stages (Fig. 3).

Nymphal development rates.—Nymphs developed faster when reared at higher temperatures (Fig. 1), and this was true for all instars and temperatures tested (Fig. 4). For each instar, development rate was a linear function of temperature (Fig. 4). Extending these development regression lines to the x-axis gives us the theoretical low temperature threshold for development. Note that these values converge to ~13°C for each of the three tested instars, and also for the total (3rd-to-adult molt) development period (Fig. 4).

Effect of temperature on adults.—Temperature strongly influenced adults. At 18°C no mating occurred; males failed to mount females. At 21°C, males mated, although significantly later than at higher temperatures ($F=18.80, n=10, P<0.05$), but females did not lay eggs (Table 1). At the three warmest temperatures, first mating averaged ~ 11 d after the adult molt. No males mated before 10 d. Throughout the experiment, both sexes mated repeatedly. Temperature influenced the pre-oviposition period, with 30°C-females laying significantly earlier (12.7 d) than 24°C-females (14.6 d) ($F=2.89, n=10, P<0.05$). No females laid before 10 d.

There was a strong nonsignificant trend ($F=1.35, n=39, P>0.05$) for females to eclose with higher mass at higher temperatures (Table 2). Likewise, comparing just the three highest temperature treatments, there was a nonsignificant trend ($F=1.35, n=39, P>0.05$) for

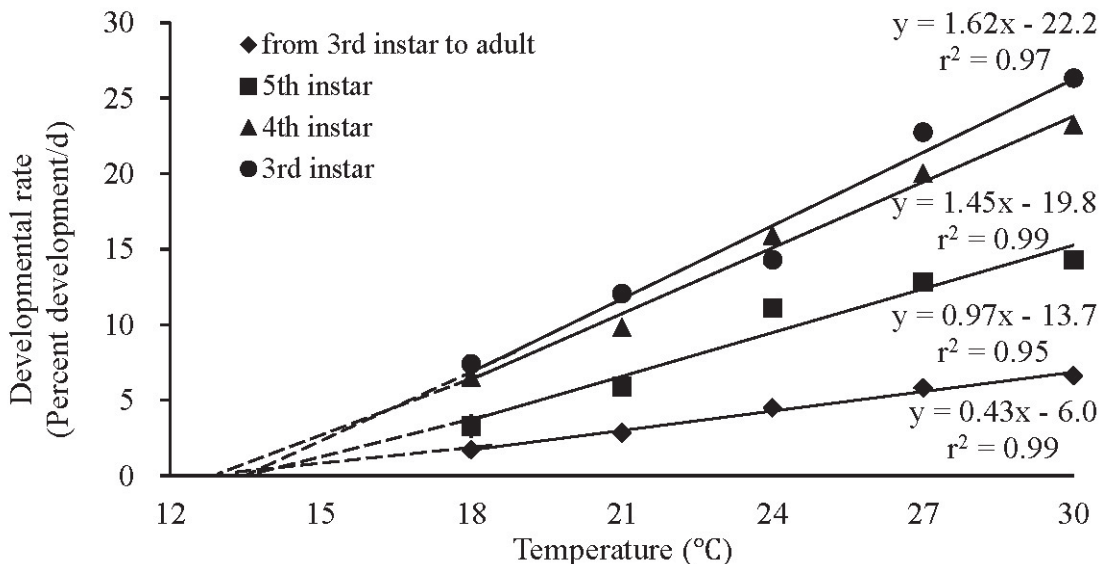


Fig. 4. Relationship between temperature and nymphal developmental rate. Dashed lines show theoretical extension of regression lines to x-axis. The points where the lines intersect the x-axis represent the Theoretical Low Temperature Threshold for Development.

Table 1. Age at mating and oviposition for *L. m. manilensis* locusts reared at different temperatures.

Temperature (°C)	Interval (days)		
	Adult molt to mating	Mating to 1 st oviposition	Adult molt to 1 st oviposition
18	No mating	No oviposition	No oviposition
21	17.0 ± 0a	No oviposition	No oviposition
24	11.3 ± 0.9b	3.3 ± 0.4	14.6 ± 1.2a
27	10.4 ± 0.2b	2.7 ± 0.3	13.1 ± 0.4ab
30	10.4 ± 0.2b	2.3 ± 0.4	12.7 ± 0.3b

^{a,b,c} Means with different letter superscripts are significantly different a $p < 0.05$, ANOVA.

females to achieve both higher pre- and postoviposition masses at higher temperatures (Table 2); females from warmer treatments tended to lose more mass during oviposition, and thus lay heavier egg masses, as determined by dry mass (Table 2).

Adults tended to live longer at warmer temperatures, with 30°C males and females surviving 67 and 63 d, respectively as adults (Table 3). This longer lifespan gave 30°C-females a longer oviposition period (= days between 1st and last egg pod). The longer oviposition period, coupled with shorter interpod intervals, allowed 30°C-females to average 12.3 pods/female, compared to only 7 pods/female for 24°C females. Hence, 30°C females produced a pod every 3.8 d, on average. At 30°C, the trends for a higher rate of pod production and greater mass/pod were reflected in a nonsignificant trend for greater overall lifetime egg deposition by 30°C-females, as measured by total dry mass of eggs deposited/female (Table 3). Indeed, the 30°C-females deposited 2.2 times as much egg mass as the 24°C-females (2.29 g *vs* 1.04 g dried egg mass/female) (Table 3).

Discussion

Temperature strongly influences all aspects of grasshopper biology (Dudley 1964; Uvarov 1966, 1977; Begon 1983; Chappell & Whitman 1990), as it does other insects (Heinrich 1993; Chown & Nicolson 2004). Numerous authors have already explored the temperature relationships of various subspecies of the Migratory Locust, *Locusta migratoria* (Hamilton 1936, 1950). Less work has been completed on the Oriental Migratory Locust, *L. m. manilensis* (Meyen) (Ma 1958; Huang & Long 1962; Huang *et al.* 1965; Wang *et*

al. 1988; Tu *et al.* 2010). In the current study, we examined the effects of constant low temperatures on nymphal growth, development, and behavior, and on adult mating, oviposition, and longevity of *L. m. manilensis*.

Our results show that at the temperatures and instars tested (18°C to 30°C and 3rd through 5th instars), nymphal growth and development rates are both linear, positive functions of temperature (Figs 3, 4). Extending these temperature *vs* rate lines to the x-axis, gives the theoretical low temperature thresholds for growth and development, which are ~ 15°C and 13°C, respectively (Figs 3, 4). These relatively high theoretical thresholds (in comparison to other insects) have significance for understanding *L. m. manilensis* in nature, because they suggest that low temperatures severely limit the ability of this pest to develop in cool climates or high latitudes. For example, at 18°C, the last three nymphal stages require ~ 60 d for completion, but only 15 d at 30°C. Hence, this subspecies appears to be adapted to warm climates. This explains why *L. m. manilensis* can complete four generations per year in southern China and the Philippines, but only one generation at 40°N latitude. Previous work suggested that the suitable developmental temperature range of *L. m. manilensis* was 25-40°C, and the optimal range was 28-34°C (Ma 1958).

The adult stage is also harmed by low temperature: at 18°C no mating occurred, at 21°C and below females were unable to lay eggs, and at 24°C, adult females laid their first egg pod significantly later than at 30°C (Table 1). There were also strong, but nonsignificant trends for low-temperature females to die earlier and lay fewer and lighter egg pods (Tables 2, 3). Indeed, 24°C-females averaged less than half the dry lifetime egg mass as 30°C-females (Table 3).

These laboratory findings can inform us about the performance of the Oriental Locust in nature. At low temperatures they will require longer time periods to complete each developmental stage. This could affect their survival under natural conditions, because they would be more vulnerable to time-dependent sources of mortality, such as exposure to pathogens or attack from natural enemies (Roy *et al.* 2002); they could also be negatively affected by other factors such as photoperiod, precipitation and food scarcity, which often affect population dynamics (Li *et al.* 1998; Kingsolver *et al.* 2006; Raworth & Schade 2006; Tu *et al.* 2010). Females that mature late in the season may be unable to lay many egg pods before the onset of winter.

Taken together, our results suggest that *L. m. manilensis* is greatly

Table 2. Mean eclosion mass, pre- and postoviposition live mass, and mean dry mass of the 1st egg batch laid for *L. m. manilensis* females maintained at different temperatures. Temperature had no significant effect on mass for any of the five variables (ANOVA, $p > 0.05$).

Temperature (°C)	Adult eclosion	Pre-oviposition	Mass (g)		
			Postoviposition	Mass lost during oviposition	1st pod dry mass
18	1.06 ± 0.09	No eggs laid	No eggs laid	No eggs laid	No eggs laid
21	1.15 ± 0.02	No eggs laid	No eggs laid	No eggs laid	No eggs laid
24	1.21 ± 0.07	2.54 ± 0.23	2.31 ± 0.20	0.20 ± 0.05	0.150 ± 0.005
27	1.27 ± 0.12	2.58 ± 0.25	2.37 ± 0.20	0.31 ± 0.04	0.182 ± 0.015
30	1.23 ± 0.03	2.67 ± 0.08	2.50 ± 0.05	0.33 ± 0.04	0.190 ± 0.024

Table 3. Mean longevity of adults, mean length of oviposition period (interval between 1st and last egg pod laid) and mean number of pods laid/female, at different temperatures. Temperature had no significant effect on any of the five variables (ANOVA, $p > 0.05$).

Temperature (°C)	♂ longevity (d)	♀ longevity (d)	Oviposition period (d)	Total pods laid per female	Dry mass of all eggs laid per female
24	49.8 ± 6.0	54.0 ± 2.1	31.0 ± 3.8	7.0 ± 1.2	1.04 ± 0.11
27	55.6 ± 6.4	63.5 ± 9.6	44.3 ± 15.2	10.5 ± 2.3	2.05 ± 0.48
30	66.8 ± 8.7	62.8 ± 7.7	47.0 ± 9.7	12.3 ± 2.7	2.29 ± 0.32

limited by low temperatures and is therefore, restricted to the warm and moderate portions of southeastern Asia. Interestingly, to the north and west, the Oriental Locust is replaced by two subspecies that appear to be more cold adapted. To the north, the Siberian or Asiatic Migratory Locust, *L. m. migratoria* L., ranges into Inner Mongolia. To the west, the Tibetan Migratory Locust, *L. m. tibetensis* Chen inhabits higher altitudes (Chen 1991).

In our study, temperature also influenced ultimate body mass, although in complex ways. For nymphs, temperatures between 21 and 30°C had little effect on mass at the adult molt. However, individuals reared at 18°C tended to be smaller at the adult molt than individuals reared at warmer temperatures (Fig. 1, Table 1). In female insects, including grasshoppers, fecundity is strongly correlated with body size (Honek 1993; Akman & Whitman 2008), and therefore it is not surprising that the smaller 18°C-females were less fecund than the larger females from warmer treatments. However, what is interesting is the stability of adult body mass from 21°C to 30°C (Figs 1, 2, Table 2). Apparently, *L. m. manilensis* has evolved to canalize body size across a wide range of temperatures. Hence, it can match growth rates and development rates over changing temperatures to produce the same target body size, possibly because that body size produces high fitness (de Jong & van der Have 2009). However, this match breaks down at low temperatures, and at 18°C, individuals reach a smaller adult size. Physiologically, size is determined by the interaction of growth rate and development rate. If development can proceed at low temperatures, but growth cannot, then the individual will continue to develop, but at a smaller size. This appears to be the case in *L. m. manilensis*, where the low temperature thresholds for development (~13°C) is lower than that for growth (~15°C) (Figs 3, 4), thus producing smaller adults at low temperatures (Figs 1, 2, Table 2).

Our data illustrate another often ignored aspect of molting in insects: insects do not feed immediately prior to and after molting. In grasshoppers, this molt-related nonfeeding period can be as long as 4 d (Rackauskas *et al.* 2006). Hence grasshoppers lose mass at this time, not only because they shed their old exoskeleton and evaporate some water, but also because they are not feeding and tend to empty their gut. This is clearly seen in Fig. 1, where average mass declines at each molt. This phenomenon is important for grasshopper control because nonfeeding grasshoppers are not harmed by ingestion-dependent insecticides. It also means that most feeding occurs in the middle of the stadium.

Our results highlight an additional important fact about insect pests of agriculture: most feeding damage is done by the last instar and adult, and less by the tiny early instars. This is seen in Fig. 2 which shows that between 21 and 30°C, well over half (~62%) of nymphal mass is acquired during the 5th (last larval) stadium. Agricultural entomologists need to adjust their management programs accordingly to address this fact.

Finally, we caution that these laboratory findings are only one factor for predicting population dynamics of locusts in the field, because of the multitude of additional variables that influence wild locusts, such as pathogens, predators, local diets, and microclimates (Uvarov 1966, 1977). In addition, locusts can, to a certain extent, regulate their body temperature via thermoregulation. Hence, air temperature is not always a good predictor of grasshopper body temperature and resulting growth, development, and fecundity rates, and thus potential for outbreak and economic damage. This is because on sunny days, grasshoppers can greatly elevate their body temperature by basking (Chappell & Whitman 1990; Lactin & Johnson 1998b). This may be why we found that *L. m. manilensis* could not complete a full generation at temperatures lower than 21°C

in the laboratory, but that in northern China, such as in Huanghua (Hebei Province) under natural conditions, this species can mature, mate and deposit eggs by early October, even though the average air temperature remains under 21°C (Ministry of Agriculture 1983). Solar basking by adults may explain this discrepancy. Likewise, locusts may physiologically acclimate, by speeding up their metabolism at cold temperatures (Whitman 2009).

In conclusion, it is clear that low environmental temperatures restrict the Oriental Locust. As such, this subspecies should not be a problem at high latitudes or altitudes, nor after periods of cool, cloudy weather during the nymphal and early adult stages. In contrast, warm and hot weather may elicit outbreaks, particularly if preceded by rains or floods, which produce suitable habitats, especially for laying eggs. We also predict that this subspecies will increase its range and damage in China as global warming increases the mean annual world temperature. It is also clear that additional comprehensive research is needed on the effects of weather on locust growth, development, survival, and movement. For example, recent results with other species of acridid indicate that temperature at the scale of individuals, has ecological consequences for intraspecific competition (Laws & Belovsky 2010).

Future research with the Oriental migratory locust should apply the results of studies such as ours, conducted on individual locusts, to develop predictions regarding population consequences. Research in this area, followed by field tests of the hypothesized relationships, could help to assess the geographic/climate distribution of habitat quality for locust populations and determine whether we can expect a trend to move to the northern or eastern regions of China (Chen & Zhang 1999; Zhang *et al.* 2003; Zhang *et al.* 2009).

Finally, the critical temperature for mating and oviposition in natural conditions needs further study with respect to biophysical models that incorporate microclimate, macroclimate, the insect body, and behavior. Climate warming, combined with insect responses under suboptimum temperatures, may modify insect development, distribution, and population dynamics, which could affect the frequency of outbreaks (Tran *et al.* 2007; Lima *et al.* 2008).

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