Environmental Entomology, XX(XX), 2020, 1–8
doi: 10.1093/ee/nvaa023
Research

Behavioral Ecology

Effect of Constant and Fluctuating Temperature on the Development, Reproduction, Survival, and Sex Ratio of *Phenacoccus solenopsis* (Hemiptera: Pseudococcidae)

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Subject Editor: Rudolf Schilder

Received 13 November 2019; Editorial decision 18 February 2020

Abstract

Effects of temperature on the development, survival, reproduction, longevity and sex ratio of the cotton mealybug, *Phenacoccus solenopsis* Tinsley, was assessed at five constant temperatures ranging from 20 to 35°C and five fluctuating temperatures ranging from 15 to 40°C under laboratory conditions. Results showed that nymphal development duration, preoviposition period, oviposition period, fecundity, and adult longevity were reduced significantly with increasing temperature until 30°C, but developmental duration of third female nymphal instar and female adult longevity was longer at 35°C than 30°C, and no males could emerge from pupae at the constant temperature 35°C. Fluctuating temperature, in general, significantly accelerated the nymphal developmental duration, prolonged preoviposition period, shortened oviposition period, reduced fecundity, lowered the survival rate of nymphs, and decreased adult longevity of males and females compared to their mean corresponding constant temperature. Overall, it is suggested that one should be prudent when applying the obtained results under constant and fluctuating temperatures under laboratory conditions.

Key words: *Phenacoccus Solenopsis* Tinsley, constant temperature, daily fluctuating temperature, survival rate, sex ratio

The cotton mealybug, *Phenacoccus solenopsis* Tinsley, was first reported by Tinsley (1898) in the United States. It is a small sucking pest of house plants and field crops, including important cash crops and forest trees. It produces honeydew on the plant leaves during feeding that lead to sooty mold production (Wu and Zhang 2009). This pest is prevalent in warmer regions because of its rapid development and reproduction.

Physiological processes of ectothermic organisms are significantly affected by temperature. Generally, insects encounter fluctuating environmental conditions rather than constant temperatures. Naturally, hot phases occurs with photo phases (day time) while cool phases occurs with dark phases (nighttime). Unlike warm-blooded animals, ectothermic insects are unable to maintain their body temperatures, which change with fluctuations of environmental temperature. Consequently, their growth and development increase directly with a rise in temperature and slow with a decrease in temperature (Palumbo 2010, Prasad et al. 2012). Temperature showed strong relationships with organisms' life processes because of their mesophilic (4–39°C), thermophilic (55°C), and psychrophilic (<4°C) regimes (Eckenfelder 2000). Biological parameters may have significant differences between fluctuating and constant temperatures under the same average temperature. As a result, data obtained under constant temperatures could not be used in predicting the occurrence of *P. solenopsis*. Many studies on the life history of *P. solenopsis* were conducted at constant temperatures on different host plants due to its polyphagous nature (Asifa et al. 2012, Prasad et al. 2012, Fand et al. 2014), but very little information or no information is available at fluctuating temperatures. Therefore, it is necessary to evaluate the biological parameters of *P. solenopsis* Tinsley not only at constant temperatures, but also at fluctuating temperatures. In nature, daily temperatures are not constant but fluctuating. Arguably, fluctuating temperatures are more relevant to what these organisms face in the field (Lamb 1961, Hagstrum and Hagstrum 1970). Biological studies of mealybugs at constant temperatures are not close to natural environmental conditions. Temperature is characterized by cyclic change. Fluctuating temperatures strongly affects the insect pest's life cycle

and interaction with plants (Pétavy et al. 2004). Exposure to fluctuating temperatures during insect development can significantly influence the nymphal growth, development, and subsequent adult fitness (Lyons et al. 2013, Warren and Anderson 2013, Wu et al. 2015). These thermal cycles can be effectively determined by using fluctuating temperatures on *P. solenopsis* under laboratory conditions. Without accounting for these variables, it is impossible to make a correct estimation of the developmental duration (Carrington et al. 2013). Several studies have been conducted on the effect of constant and fluctuating temperatures on the insect life cycle (Davis et al. 2006, Bahar et al. 2012, Carrington et al. 2013), but this is the first time we are describing fluctuating temperature effects on the biology of *P. solenopsis*.

In this experiment, a detailed study was carried out on the life history of *P. solenopsis* at constant and fluctuating temperatures. Nymphal developmental duration, female preoviposition and oviposition duration, fecundity, longevity, survivorship and sex ratio of *P. solenopsis* were determined. The overall objective of this study was to provide basic information and to better understand the *P. solenopsis* life history under constant and fluctuating temperatures and to determine proper management practices.

Materials and Methods

Host Plant and Insect Source

The colony of mealybug was maintained on a tomato plant (*Solanum lycopersicum*) as the host, at 27 ± 1°C and 60–75% RH, under a photoperiod of 12:12 (L: D) h. Plants were grown in plastic pots (13-cm diameter) with field soils in a climate room at 27 ± 1°C, 60–75% RH, and a photoperiod 12:12 (L:D) h. All plants used in the study initially had five to seven fully expanded true leaves.

Development and Reproduction Under Constant Temperature

Biological parameters of *P. solenopsis*, were set and assessed under constant temperatures of 20, 25, 27, 30, and 35°C, under a photoperiod of 12:12 (L:D) h with 50–65% humidity in an environmental growth chamber. For each temperature, 40–50 fertilized females were collected from the colony and transferred onto the tomato plants in the growth chamber with the objective being to obtain eggs or neonate crawlers to facilitate for later study of the developmental cycle. Observations were made daily for fecundity and collections of neonate crawlers were carried out as indicated. Ten newly emerged neonate crawlers were collected from the female ovisac with the help of camel hair brush and transferred onto fully grown tomato leaves in the growth chamber. Observations were made daily to observe the nymphal instar molting. Complete molting of one instar into the next instar was counted as the completion of an instar developmental period. Shedded skin was the clear evidence of nymphal instar molting and these skins were present near the molted nymphs. The date nymphs molted into the next instar or stage was recorded on the plant pots. Nymphs that molted on the same day were transferred onto new plants and reared separately. Sex differentiation between female and male was determined after the molting of second instar into third instar and after the complete molting of second instar into pupal form, respectively. From this stage onward, female and male developmental duration was recorded separately. After the third nymphal stage, female nymphs molted into the adult stage and males emerged out form puparium into their winged adult forms. Cumulative developmental duration of males and females was computed from crawler to adult emergence. Tomato plants being maintained at a higher temperature of 35°C and low temperature of 20°C were changed as required. Twelve replicas were carried out at each temperature. After the emergence of male and female adults, one male and one female were paired in plastic box. Preoviposition period (time from adult emergence to start of egg laying), oviposition period (time from start to end of egg laying), fecundity (number of eggs produced by each female), and adult longevity of both females and males was recorded daily. For reproductive parameters, at least 30 adults of each sex were inspected and recorded. Additional males and females were also reared separately to obtain more pairs for reproduction parameters. Temperature and humidity of the growth chamber was also measured constantly with temperature and humidity meters.

Development and Reproduction Under Fluctuating Temperature

Development and reproduction of *P. solenopsis* was studied at four fluctuating temperatures and four constant temperatures (27.5, 28.75, 31, and 33°C). Fluctuating temperatures were further divided into wide fluctuating temperature (8°C differential) and narrow fluctuating temperatures (5°C differential). The wide fluctuating temperature was set at 27–35°C with mean of 31°C, and 27–35 °C with mean of 33°C. Narrow fluctuating temperatures were 25–30°C with mean of 27.5°C and 25–30°C with mean of 28.75°C. Mean corresponding constant temperature of both wide and narrow fluctuating temperature was considered as the control. For each temperature experiment, 25–35 mated females were collected from the colony and transferred onto the tomato plants in growth chambers to obtain eggs or neonate crawlers to study the duration of development. Observation and collection of data regarding nymphal development durations as well as reproduction were recorded in the same fashion as mentioned above in development and reproduction under constant temperature.

Survival Rate and Sex Ratio Under Constant and Fluctuating Temperature

Effects of constant and fluctuating temperatures on survival rate were evaluated at five constant and five fluctuating temperatures. Constant temperatures, 20, 25, 27.5, 30, and 35°C were designed to observe survival rate. Similarly, fluctuating temperature also 20, 25, 27.5, 30, and 35°C were designed. To get corresponding fluctuating temperature, insects were exposed to both low and high temperatures for 12 h each day. For example, to get 20°C fluctuating temperature, insects was cultured 12 h at 15°C and 12 h at 25°C each day. Fluctuating temperatures was 15–25°C with mean of 20°C, 20–30°C with mean of 25°C, 25–30°C with mean of 27.5°C, 25–35°C with mean of 30°C, and 30–40°C with mean of 35°C.

Sex ratio were determined at five constant temperatures ranging from 20 to 35°C and five fluctuating temperature ranging from 20 to 35°C. Six replications were maintained at each temperature. At each replicates, 60 to 75 freshly emerged first nymphal instar were introduced on tomato plant leaves and exposed to different assigned temperature. Individual numbers of each instar survived to next instar at each temperature was recorded and used to calculate the survival rate. Total nymphal survival rate was calculated with the adult number of both male and female divided by the number of nymph used at the beginning of experiment.

Statistical Analysis

One-way analysis of variance (ANOVA) was carried out by using linear general model procedure PROC GLM (SAS Institute Inc. 2009)

to discern the effects of constant and fluctuating temperature on the development, reproduction and survival of *P. solenopsis*. Variable means were separated by using Tukey's honestly significant difference (HSD) test with $P = 0.05$ significance level. Sex ratio comparison was discerned by *t*-test.

Results

Development and Reproduction Under Constant Temperature

Developmental durations of nymphs in each instar are presented in Table 1. Data analysis showed that constant temperature has significant effect on the nymphal duration, pupal duration, and cumulative female and cumulative male developmental duration. As assumed, developmental duration significantly decreased with increasing temperature (first instar: $F = 1418.22$, degrees of freedom (df) = 4, $P \leq 0.0001$; second instar: $F = 853.37$, df = 4, $P \leq 0.0001$; third instar: $F = 1713.87$, df = 4, $P \leq 0.0001$). Developmental durations of nymphs in first, second and third at 20 ± 1°C was exactly 2.6, 2.1, and 1.9 times longer than those at 35 ± 1°C, respectively. There was no obvious characteristics to differentiate sexes at first- and second-instar stages; therefore, developmental duration of both sexes are combined together at this stage. Longest nymphal duration of first and second instars was observed at 20°C and shortest at 35 ± 1°C. The males which developed from second instar into pupae could not survive at 35°C. For the females, longest developmental duration of third nymphal instar was noticed at 20 ± 1°C and shortest at 30 ± 1°C. Developmental duration of third nymphal instar and cumulative duration of female were longer at 35°C than those at 30 ± 1°C, suggesting that 35°C temperature may be little bit higher for female nymphal development.

Pre-oviposition period, oviposition period, fecundity, and female longevity were significantly affected from the all temperatures. All females undergo reproduction phase at all temperatures except 35°C because there was no males emerged from puparium. Both preoviposition ($F = 487.15$, df = 3, $P \leq 0.0001$) and oviposition ($F = 140.13$, df = 3, $P \leq 0.0001$) periods reduced significantly with raising temperature. Longest preoviposition and oviposition duration was recorded at 20°C and shortest was recorded at 30°C. Adult female can produce offspring at a temperature range of 20–30°C, but their numbers of offspring decreased significantly with increasing temperature. However, adult female emerged at 35°C cannot produce any offspring without male. Highest fecundity (174.5 ± 10.8 crawlers per female) was recorded at 20°C and lowest (90.9 ± 18.5 crawlers per female) was recorded at 30°C. Longevity of adult female decreased significantly ($F = 1857$, $P \leq 0.0001$) from 42.7 ± 1.1 d at 20°C to 19.6 ± 0.7 d at 30 °C, but it was longer at 35°C than that at 30°C. Male longevity decreased significantly with increasing temperature (Table 2). Its relationship with temperature was similar to that of female.

Development and Reproduction Under Daily Fluctuating Temperature

Phenacoccus solenopsis Tinsley successfully completed their whole life cycles on the all fluctuating and constant temperatures (Tables 3 and 4). Both fluctuating and their corresponding constant temperatures showed significant effects on the life parameters of mealybug. Narrow fluctuating temperature significantly effects the first-instar ($F = 19.90$, df = 3, $P \leq 0.0001$), second-instar ($F = 373.78$, df = 3, $P \leq 0.0001$), third-instar nymph ($F = 146.28$, df = 3, $P \leq 0.0001$), male pupae ($F = 64.02$, df = 3, $P \leq 0.0001$), and whole nymphal instar durations ($F = 404.28$, df = 3, $P \leq 0.0001$). Both narrow and wide fluctuating temperatures reduced the nymphal duration when compared with their corresponding constant temperature (Tables 3 and 4). At narrow fluctuating temperature, *P. solenopsis* female nymphs completed their development within 14.2 ± 0.8 d at 28.75°C, while they completed their nymphal duration within 20.1 ± 0.4 d at mean corresponding constant temperature. Similar trends have been noticed at another narrow fluctuating temperature and at wide fluctuating temperatures. Overall, total nymphal survival was lower at fluctuating temperatures compared with constant temperature.

Significant differences was noticed on preoviposition period, oviposition period, fecundity, and longevity between constant and both narrow and wide fluctuating temperature. In general, fluctuating temperature prolonged the preoviposition period, decreased oviposition period, reduced fecundity, and shortened longevity (Tables 5 and 6). However, some variability was also noticed when compared with their corresponding constant temperature such as at fluctuating temperature 27.5°C, male longevity did not decreased (Table 5), at fluctuating temperature 28.75°C, fecundity and female longevity did not reduced (Table 5), and at higher temperature (33°C), fluctuating temperatures did not increase the preoviposition period (Table 6).

Effects of Constant and Fluctuating Temperature on the Survival Rate and Sex Ratio

Both constant and fluctuating temperature significantly affect the survivals of *P. solenopsis* at nymphal stages (first instar, $F = 68.93$, df = 9, $P \leq 0.0001$; second instar, $F = 9.67$, df = 9, $P \leq 0.0001$; third instar, $F = 7.82$, df = 9, $P \leq 0.0001$, whole nymphal stage, $F = 55.76$, df = 9, $P \leq 0.0001$; Table 7). Most of fluctuating temperatures decreased the nymphal survival rates when compared with their corresponding constant temperature. The nymphs in first instars had lower survival rates when compared with second and third nymph instars, especially at lowest and highest temperatures, suggesting that they are highly susceptible to extreme temperatures.

Table 1. Developmental duration in days (mean± SD) of nymphal instars on the constant temperatures

Temperature (°C)	Male and female		Female third nymphal Instar	Male pupae	Female cumulative nymphal duration	Male cumulative duration
	First nymphal instar	Second nymphal instar				
20	13.4 ± 0.4a	14.3 ± 0.4a	14.5 ± 0.3a	14.5 ± 0.3a	42.2 ± 0.5a	42.2 ± 0.8a
25	7.0 ± 0.3b	8.1 ± 0.2b	8.0 ± 0.3b	8.2 ± 0.2b	23.3 ± 0.5b	23.6 ± 0.5b
27	6.6 ± 0.1c	7.5 ± 0.1c	6.0 ± 0.1d	6.8 ± 0.2c	20.2 ± 0.6c	21.0 ± 0.3c
30	6.5 ± 0.1c	7.0 ± 0.2d	5.8 ± 0.3d	6.1 ± 0.2d	19.3 ± 0.5d	19.7 ± 0.3d
35	5.2 ± 0.2d	6.9 ± 0.1d	7.5 ± 0.2c	-	19.8 ± 0.4cd	-

Means within a column followed by the same letters are not significantly different at $P < 0.05$ (Tukey's HSD test).

Table 2. Female reproduction parameters and adult longevity (mean± SD) at different constant temperatures

Temperature (°C)	Female				Male Longevity (days)
	Pre-oviposition period (days)	Oviposition period (days)	Fecundity (offspring/♀)	Longevity (days)	
20	20.5 ± 0.9a	18.5 ± 1.0a	174.5 ± 10.8a	42.7 ± 1.1a	4.5 ± 0.4a
25	15.7 ± 0.9b	10.5 ± 1.0b	142.5 ± 8.2b	29.2 ± 0.9b	4.0 ± 0.2b
27	11.0 ± 0.6c	11.5 ± 1.0b	130.0 ± 16.0c	27.1 ± 0.8d	3.7 ± 0.1c
30	9.0 ± 0.5d	8.7 ± 1.5c	90.9 ± 18.5d	19.6 ± 0.7e	3.4 ± 0.2d
35	–	–	–	27.9 ± 1.0c	–

Means within a column followed by the same letters are not significantly different at $P < 0.05$ (Tukey's HSD test).

Table 3. Developmental duration in days (mean± SD) of nymphal instars under the narrow range fluctuating temperatures and the corresponding constant temperatures

Temperature (°C)*	Male and female		Female third nymphal instar	Male pupae	Cumulative nymphal	
	First nymphal instar	Second nymphal instar			Female	Male
FT27.5	6.2 ± 0.4b	6.0 ± 0.2c	5.7 ± 0.4d	6.0 ± 0.1b	18.0 ± 0.3b	18.3 ± 0.3c
CT27.5	6.6 ± 0.2a	7.4 ± 0.3a	6.1 ± 0.1b	6.8 ± 0.1a	20.1 ± 0.6a	20.9 ± 0.3a
FT28.75	5.6 ± 0.2c	4.0 ± 0.1d	4.5 ± 0.2c	4.8 ± 0.2c	14.2 ± 0.8c	14.4 ± 0.4d
CT28.75	6.2 ± 0.2b	7.1 ± 0.3b	6.7 ± 0.1a	6.7 ± 0.1a	20.1 ± 0.4a	20.2 ± 0.4b

FT27.5: 27.5°C at fluctuating temperature (12 h at 30 °C, 12 h at 25 °C); CT27.5: 27.5°C at constant temperature; FT28.75:28.75°C at fluctuating temperature (18 h at 30 °C, 6 h at 25 °C); CT28.75: 28.75°C at constant temperature. Table 5 is the same. Means within a column followed by the same letters are not significantly different at $P < 0.05$ (Tukey's HSD test). Significant were marked by $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Table 4. Developmental duration in days (mean± SD) of nymphal instars under the wide range fluctuating temperatures and the corresponding constant temperatures

Temperature (°C)*	Male and female		Female third nymphal instar	Male Pupae	Cumulative nymphal	
	First nymphal instar	Second nymphal instar			Female	Male
FT31	5.5 ± 0.3b	5.3 ± 0.4b	5.5 ± 0.3b	5.3 ± 0.2b	16.3 ± 0.3b	16.1 ± 0.3b
CT31	6.2 ± 0.2a	6.0 ± 0.2a	6.0 ± 0.2a	6.0 ± 0.2a	18.3 ± 0.2a	18.3 ± 0.2a
FT33	4.2 ± 0.2d	3.5 ± 0.2d	4.2d ± 0.2d	4.3 ± 0.3d	12.0 ± 0.5d	12.2 ± 0.4d
CT33	5.0 ± 0.1c	4.3 ± 0.3c	4.7 ± 0.1c	4.7 ± 0.1c	14.0 ± 0.3c	14.0 ± 0.4c

FT31: 31°C at fluctuating temperature (12 h at 35°C, 12 h at 27°C); CT31: 31°C at constant temperature; FT33:33°C at fluctuating temperature (18 h at 35°C, 6 h at 27°C); CT33: 33°C at constant temperature. Table 6 is the same. Means within a column followed by the same letters are not significantly different at $P < 0.05$ (Tukey's HSD test). Significant were marked by $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Table 5. Female reproduction parameters and adult longevity (mean± SD) at different narrow range fluctuating temperatures and the corresponding constant temperatures

Temperature (°C)	Pre-oviposition period (d)	Oviposition period (d)	Fecundity (offspring/♀)	Longevity (d)	
				♀	♂
FT27.5	11.9 ± 0.9b	5.5 ± 0.5b	70.0 ± 7b	19.7 ± 1.1b	3.3 ± 0.2b
CT27.5	10.3 ± 0.8c	10.8 ± 1.0a	95.7 ± 10.6a	22.5 ± 1.1a	3.4 ± 0.2b
FT28.75	13.2 ± 0.5a	4.2 ± 0.4d	67.8 ± 6.4b	18.8 ± 0.6c	2.8 ± 0.2c
CT28.75	10.8 ± 0.8c	5.0 ± 0.5c	74.3 ± 11.0b	18.4 ± 1.2c	3.7 ± 0.2a

Means within a column followed by the same letters are not significantly different at $P < 0.05$ (Tukey's HSD test).

Phenacoccus solenopsis successfully develop at all constant and fluctuating temperature in this experiment. Comparison of male-to-female ratio by *t*-test showed that at all temperature, the sex ratio is variable. There are more females than males at lowest constant and fluctuating temperature, 20°C, and at highest constant temperatures, 35°C (Table 8). There was no male at constant temperature 35°C because all male died during pupal stage. The negative *t*-value showed that males have less percentage than females whereas the positive *t*-value vice versa. All constant temperatures except 30°C significantly affect the sex ratio whereas all fluctuating temperatures except 20°C nonsignificantly affect the sex ratio. There are more females at the all constant temperatures except 30°C and at all fluctuating temperatures except 27.5°C.

Table 6. Female reproduction parameters and adult longevity (mean± SD) at different wide range fluctuating temperatures and the corresponding constant temperatures

Temperature (°C)	Pre-oviposition period (d)	Oviposition period (d)	Fecundity (offspring/)	Longevity (d)	
				♀	♂
FT31	8.2 ± 0.5a	4.5 ± 0.6c	82.9 ± 7.1b	14.6 ± 0.5b	2.5 ± 0.3b
CT31	8.0 ± 0.4b	7.0 ± 0.7a	104.0 ± 11.5a	16.7 ± 0.6a	3.0 ± 0.2a
FT33	7.2 ± 0.5c	4.0 ± 0.4d	80.2 ± 14.4b	12.5 ± 0.6c	2.0 ± 0.2c
CT33	8.0 ± 0.5b	5.5 ± 0.7b	103.4 ± 25.4a	14.9 ± 0.4b	3.0 ± 0.2a

Means within a column followed by the same letters are not significantly different at $P < 0.05$ (Tukey's HSD test).

Table 7. Percent survival (mean ± SD) of different nymphal instars of *P. solenopsis* at different constant and fluctuating temperatures

Temperature (°C)	First instar (♀ and ♂)	Second instar (♀ and ♂)	Third instar (♀)	First-instar adult (♀ and ♂)
FT20	45.4 ± 3.5d	81.6 ± 3.0c	86.0 ± 4.3b	32.9 ± 4.8e
CT20	62.8 ± 4.3b	78.6 ± 3.0d	89.7 ± 3.3a	45.5 ± 5.0d
FT25	74.5 ± 2.8a	84.9 ± 2.1b	87.4 ± 3.1b	55.6 ± 2.8b
CT25	74.4 ± 3.4a	89.9a ± 1.4a	92.9 ± 2.3a	63.6 ± 3.2a
FT27.5	75.5 ± 3.3a	82.4 ± 2.5c	86.8 ± 2.1b	55.4 ± 4.5b
CT27.5	80.8 ± 3.7a	89.1b ± 2.9a	83.8 ± 3.1b	61.1 ± 5.3a
FT30	67.6 ± 4.3b	81.4 ± 16.0c	88.7 ± 3.4b	48.6 ± 4.3d
CT30	75.0 ± 4.0a	81.0 ± 5.0c	86.4 ± 2.5b	53.8 ± 2.7c
FT35	51.3 ± 2.7c	75.6 ± 4.0e	80.5 ± 2.9c	32.0 ± 2.1e
CT35	55.5 ± 2.5c	86.0 ± 1.4b	80.4 ± 5.5c	34.2 ± 2.5e

FT20:20°C at fluctuating temperature (12 hat 25°C, 12 h at 15°C); CT20: 20°C at constant temperature; FT25: 25°C at fluctuating temperature (12 hat 30°C, 12 h at 20°C); CT25: CT25°C at constant temperature; FT27.5: 27.5°C at fluctuating temperature (12 h at 30°C, 12 h at 25 °C); CT27.5: 27.5°C at constant temperature; FT30: 30°C at fluctuating temperature (12 h at 35°C, 12 h at 25°C); CT30: 30°C at constant temperature; FT35: 35°C at fluctuating temperature (12 h at 40°C, 12 h at 30°C); CT35: 35°C at constant temperature. Means within a column followed by the same letters are not significantly different at $P < 0.05$ (Tukey's HSD test).

Table 8. Comparison of temperature dependent sex ratio of *P. solenopsis* by *t*-test

Temperature (°C)	Percentage of male	Percentage of female	*t*-value	df	*P*-value
20 FT	32.3 ± 4.6	67.7 ± 4.6	-5.431	10	<.0001
20 CT	34.0 ± 1.3	66.0 ± 1.3	-16.965	10	<.0001
25 FT	49.1 ± 5.0	50.9 ± 5.0	-.251	10	.807
25 CT	44.1 ± 2.0	55.9 ± 2.0	-4.126	10	.002
27.5 FT	55.6 ± 2.9	44.4 ± 2.9	+2.771	10	.020
27.5 CT	41.1 ± 1.9	58.9 ± 1.9	-6.784	10	<.0001
30 FT	43.6 ± 4.6	56.4 ± 4.6	-1.955	10	.079
30 CT	54.4 ± 3.5	45.6 ± 3.5	+1.77	10	.107
35 FT	50.9 ± 3.5	49.1 ± 3.5	+.358	10	.728
35 CT	-	100	-	-	-

FT20: 20°C at fluctuating temperature (12 h at 25°C, 12 h at 15°C); CT20: 20°C at constant temperature; FT25: 25°C at fluctuating temperature (12 h at 30°C, 12 h at 20°C); CT25: 25°C at constant temperature; FT27.5: 27.5°C at fluctuating temperature (12 h at 30 °C, 12 h at 25°C); CT27.5: 27.5°C at constant temperature; FT30: 30°C at fluctuating temperature (12 h at 35°C, 12 h at 25°C); CT30: 30°C at constant temperature; FT35: 35°C at fluctuating temperature (12 h at 40°C, 12 h at 30°C); CT35: 35°C at constant temperature.

Discussion

Being ectothermic organisms, insects are more susceptible to changes in rate of growth, development, survival, fecundity, and longevity with changing temperature. *Phenacoccus solenopsis* is a harmful pest to a wide range of flowers, important cash crops and plants. The host plant is also another important factor affecting physiology and behavior of insects. Some scientists have investigated the effects of temperature and humidity on *P. solenopsis* on cotton (Vennila et al. 2010, Prasad et al. 2012, Kumar et al. 2013), China rose (*Hibiscus rosasinensis*) (Asifa et al. 2012), and other host plants (Suroshe et al. 2016).

In our experiment, results on tomato plant as the host showed that both constant and fluctuating temperatures affect the development, reproduction, survival rate, and sex ratio of *P. solenopsis*. A high temperature of 35°C proved detrimental for the male pupae survival. No male survived to adult at this temperature. Without males, females did not produce offspring at this temperature. Therefore, on a small scale (green houses), manipulating environmental temperature until 35°C or a little bit higher may be a viable and ecologically friendly control practice for the management of this pest in china.

Progressively higher constant temperatures increasingly reduced the nymphal instar duration when comparing 20°C with 30°C; however, the high temperature of 35°C proved detrimental to female reproduction. Our results are not consistent with reports of Prasad et al. (2012) and Ali et al. (2012), because in their study male

nymphs developed into adults. This may be due to different plant species and geography, as we used tomato plant for a host while cotton and China rose was used in their study. *Phenacoccus solenopsis* females completed their whole nymphal stages in 42.2 d at 20 ± 1°C, 23.3 d at 25 ± 1°C, 20.2 d at 27 ± 1°C, 19.3 d at 30 ± 1°C, and 19.8 d at 35 ± 1°C. Chong et al. (2008) reported that cumulative nymphal duration was 66.4 ± 0.4 d at 20°C, 31.3 ± 0.4 d at 25°C, 29.2 ± 0.4 d at 27°C, and 33.3 ± 0.7 d at 30°C. Asifa et al. (2012) reported that developmental duration of nymphal stages was longer at low temperatures and was shorter at higher temperatures. This can be explained by the fact that high temperatures increase the metabolic rates and low temperature reduced the metabolic rates, and consequently insect developmental durations vary according to these temperature changes (Davidowitz and Nijhout 2004, Andreadis et al. 2013).

In our study, preoviposition period, oviposition period, and fecundity of *P. solenopsis* were significantly reduced with increasing the temperature from 20 to 30°C. Our findings are consistent with Ali et al. (2012) findings on *P. solenopsis* but not consistence with reports on *P. solenopsis* that were reared on cotton (Prasad et al. 2012).

Narrow and wide fluctuating temperatures have a profound effect on the biology of *P. solenopsis*. Results indicated that effects of fluctuating temperatures differed from constant temperature effects. Both narrow and wide fluctuating temperature shortened the total nymphal instar duration of *P. solenopsis*. Our results are consistent with reports on *Tribolium castancum* Herbst (Coleoptera: Tnenebrionidae) and *Trogoderma inclusum* LeConte (Coleoptera: Dermestidae) (Hagstrum and Leach, 1973), *Lycaena tityrus* Poda (Lepidoptera: Lycaenidae) (Fischer et al. 2011), *Anopheles funestus* Giles (Diptera: Culicidae) (Lyons et al. 2013), *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae) (Mironidis and Savopoulou-Soultani 2014), and *Venturia canescens* Gravenhorst (Hymenoptera: Ichneumonidae) (Spanoudis et al. 2015) but not consistent with reports on green peach aphid (Davis et al. 2006) and *Anopheles arabiensis* Giles (Diptera: Coleoptera) (Lyons et al. 2013). The mechanism of insects' faster growth and development at variable temperatures is currently not clear, but the possible reason might be related to more food consumption during daytime due to high temperatures and less food consumption during night time due to low temperature due to decreased metabolic losses at this time (cf. Kingsolver and Woods 1997, Renault et al. 2002, Karl and Fischer 2008). *Helicoverpa armigera* (Hübner) pupae develop rapidly at the fluctuating temperature when compared with at a mean constant temperature of 24°C (Foley 1981). Insects grew swiftly in the fluctuating temperature when lowest and highest alternating temperature was in medium or average range (Hagstrum and Hagstrum 1970). *Diaphorencyrtus aligarhensis* Shafee, Alam & Agarwal (Hymenoptera: Encyrtidae) females completed their development faster at a constant temperature of 15°C and slower at constant temperatures of 30 and 35°C when compared with their mean fluctuating temperature but developmental time was not significantly different between constant and fluctuating temperatures at 20, 25, and 32°C. Similarly, male developmental time was shorter at constant temperatures of 15 and 20°C when compared with their fluctuating temperature (Milosavljević et al. 2019).

Results of reproduction showed that both wide and narrow fluctuating temperatures significantly reduced the oviposition duration and fecundity of *P. solenopsis* when compared with their mean constant temperature. Our results are consistent with reports on *Zeiraphera Canadensis* Mutuura & Freeman (Lepidoptera: Tortricidae) (Carroll and Quiring 1993) but not consistent with repots on mites and insect species on green peach aphid (Davis et al. 2006), *Phytoseiulus persimilis* Evans (Mesostigmata: Phytoseiidae), *Tetranychus urticae* C. L. Koch (Trombidiformes: Tetranychidae), *Neoseiulus californicus* McGregor (Mesostigmata: Phytoseiidae) (Vangansbeke et al. 2013), and *Helicoverpa armigera* (Mironidis and Savopoulou-Soultani 2014) where higher fecundity or equal fecundity was recorded at fluctuating temperature when compared with their corresponding constant temperatures. Comparison of narrow range and wide range fluctuating temperature showed that *P. solenopsis* male and female longevities are longer at a narrow range fluctuating temperature. Similarly, adult longevity of endoparasitoid *Venturia canescens* was longer at a narrow range fluctuating temperature than a wide range fluctuating temperature (Spanoudis et al. 2015). From our findings, we suggest that field populations of *P. solenopsis* experiencing fluctuating temperatures have faster growth and development, less population growth potential, and less survival rate than populations developing at their mean constant temperature. These conclusions indicate that effects of fluctuating temperatures are very important for the forecasting of insect population dynamics and phenology.

In our experiment, constant and fluctuating temperatures of 20 and 35°C proved detrimental for the survival of *P. solenopsis*, whereas intermediate constant and fluctuating temperatures (i.e., 25, 27.5, and 30°C) proved favorable for their survival in our experiment. Fluctuating temperature reduced the survival rate of *P. solenopsis* when compared with their respective mean constant temperatures. Regarding constant temperature effects, our results are consistence with findings on *Phenacoccus madeirensis* Green (Hemiptera: Pseudococcidae) and *Maconellicoccus hirsutus* Green (Hemiptera: Pseudococcidae) (Chong et al. 2003, 2008), *P. solenopsis* reared on cotton (Prasad et al. 2012), *A. funestus* (Lyons et al. 2013) and *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) (Smaniotto et al. 2019). First nymphal instars proved highly susceptible to all constant and fluctuating temperature while second and third nymphal instars was less susceptible and had a higher survival at all temperatures. Similar findings have been reported on *P. solenopsis* in India (Prasad et al. 2012, Fand et al. 2014) and on Giant Whitefly *Aleurodicus dugesii* Cockerell (Hemiptera: Aleyrodidae: Aleurodicinae) (Schoeller and Redak 2018).

Apart from its effect on development and survival, temperature also has a strong effect on the sex ratio (Choi et al. 2015). Our results showed that temperature has profound effect on *P. solenopsis* sex ratio. There were more females at the lowest and highest temperatures, whereas there was little differentiation between male and female ratio at intermediate temperatures. This suggested that males are more vulnerable to extremes of temperature. Several studies show that temperature has a strong effect on sex allocation. Temperature-dependent sex ratio studies proved that temperature play an important in sex allocation of reptiles, birds, turtles, and fish (Goth and Booth 2005, Goto-Kazeto et al. 2006). Painted turtle (*Chrysemys picta* Schneider (Testudines: Emydidae)) produces 98% males at 28°C, whereas it produces 100% females at 29.5°C (Bull et al. 1982) and goldfish *Carassius auratus* Linnaeus generates into 100% females at 17°C, 46.6% females at 25°C, and 7.7% females at 30°C (Goto-Kazeto et al. 2006). In insects, we compare our results by temperature-dependent sex ratio. In our study, there was a female-biased sex ratio at low temperature of 20°C and very high temperature of 35°C while there was little differentiation between male-to-female sex ratio at intermediate temperatures but there was a male-biased sex ratio at a constant temperature of 30°C and fluctuating temperature of 27.5°C. This confirms the findings of scientist that temperature and pH are the key environmental factors that

have strong effect on sex differentiation (Baroiller et al. 1999, Devlin and Nagahama 2002). Our findings regarding constant temperature effects are not consistent with reports on *P. solenopsis* reared on cotton (Prasad et al. 2012) and *Hibiscus rosa-sinensis* (Sreedevi et al. 2013), because there was a female-biased sex ratio at all temperatures and female percentage was 70–97% at all constant temperatures (Prasad et al. 2012, Sreedevi et al. 2013). Temperature effect was found to be curvilinear on *P. solenopsis* sex ratio at the different temperatures and 60% humidity (Chen et al. 2015). In contrast to our results, Chen et al. 2015 found the male-biased sex ratio at the constant lowest temperature of 20°C and highest temperature of 35°C when humidity was 60%, but they found the female biased sex ratio when humidity was 45% at these same temperature.

Conclusion

Our experimental results provide new information on the effect of constant and fluctuating temperature on nymphal developmental duration, female adult longevity reproduction, male adult longevity, survival, and sex ratio of *P. solenopsis*. Our results will be helpful for understanding the population dynamics of this pest on tomato plants under fluctuating temperatures. However, except temperature effect, many other factors such as different host plant, relative humidity, food quality and quantity, light and heat shock events also affect the life cycles of *P. solenopsis*. Therefore, further investigation into the effects of environmental factors on the life cycle, survival, and sex ratio of these insects are required to allow for a more complete understanding.

Acknowledgments

We acknowledge the National Basic Research Program of China 973 Program (grant 2009CB119005 and 2006CB102005); the National 948 Program (grant 2011-G4), and the National Department Benefit Research Foundation (grant 20110321) for their generous financial support to this research.

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