Effects of temperature on the development and reproduction of *Oligonychus litchii* Lo and Ho (Acari: Tetranychidae) when reared on litchee

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Abstract

Oligonychus litchii Lo and Ho (Arachnida: Acari: Tetranychidae) is one of the primary pests in the litchi orchard and causes serious damage. We studied the effects of temperature on development and reproduction of *O. litchii* and constructed experimental population life tables at 5 constant temperatures (20, 23, 26, 29, and 32 °C) under laboratory conditions. The results showed that development, reproduction, and life table parameters of *O. litchii* were significantly affected by different temperatures. The egg stage had the longest period of development, and survival or development time decreased significantly with rising constant temperatures. Duration of the larva, protonymph, and deutonymph stages, and total generation time, tended to decline as the temperature increased, but development time at 26, 29, and 32 °C did not differ significantly. The longest generation time (egg to death of the adult) was 34.3 d at 20 °C, followed by 21.9 d at 23 °C, and it was shortest at 32 °C (10.7 d). There is a positive linear correlation between the temperature (T) and developmental rate (V). The developmental threshold temperature and effective accumulated temperatures for the entire generation were 13.4 °C and 172.41 degree-d, respectively. The highest number of eggs laid per female was 77.2 eggs at 26 °C, while the lowest was 30.0 eggs at 20 °C. The maximum population growth rate (r_m) values increased from 20 °C (0.04) to 29 °C (0.17), then decreased at 32 °C (0.12). The finite rates of increase (λ) were over 1.00 at all 5 constant temperatures. Temperature had a great effect on the development and reproduction of *O. litchi*, and the optimal temperature for the mite is around 26 °C.

Key Words: development; reproduction; developmental threshold temperature; effective accumulated temperature; life table

Resumen

Oligonychus litchii Lo y Ho (Arachnida: Acari: Tetranychidae) es una de las plagas principales en los huertos de litchi y causa daños serios. Estudiamos el efecto de la temperatura sobre el desarrollo y la reproducción de *O. litchii* y construimos tablas de vida de las poblaciones experimentales a 5 temperaturas constantes (20, 23, 26, 29 y 32 °C) bajo condiciones de laboratorio. Los resultados mostraron que los parámetros de desarrollo, reproducción y tabla de vida de *O. litchii* fueron afectados significativamente por las diferentes temperaturas. El estadio del huevo tuvo el período de desarrollo más largo y el tiempo de sobrevivencia o desarrollo disminuyó significativamente con el aumento constante de las temperaturas. La duración del estadio de la larva, protoninfa y deutoninfa y el tiempo de generación total tendieron a disminuir a medida que aumentaba la temperatura, pero el tiempo de desarrollo a 26, 29 y 32 °C no difirió significativamente. El tiempo de generación más largo (huevo hasta la muerte del adulto) fue de 34.3 días a 20 °C, seguido de 21.9 días a 23 °C, y fue lo más corto a 32 °C (10.7 días). Existe una correlación lineal positiva entre la temperatura (T) y la tasa de desarrollo (V). La temperatura de umbral de desarrollo y las temperaturas acumuladas efectivas para toda la generación fueron de 13.4 °C y 172.41 grados-dias, respectivamente. El mayor número de huevos depositados por hembra fue de 77.2 huevos a 26 °C, mientras que el más bajo fue de 30.0 huevos a 20 °C. Los valores máximos de la tasa de crecimiento de la población (r_m) aumentaron de 20 °C (0.04) a 29 °C (0.17), luego disminuyeron a 32 °C (0.12). La tasa finita de aumento (λ) fue mas de 1.00 a las 5 temperaturas constantes. La temperatura tuvo un gran efecto sobre el desarrollo y la reproducción de *O. litchii* y la temperatura óptima para el ácaro es de alrededor de 26 °C.

Palabras Clave: desarrollo; reproducción; temperatura umbral de desarrollo; temperatura acumulada efectiva; tabla de vida

Oligonychus litchii Lo and Ho (Arachnida: Acari: Tetranychidae) is a new pest of litchi (Sapindaceae) in southern China; it was first reported by Lo and Ho (1989) in Taiwan. This mite species attacks more than 30 species of host plants, including *Litchi chinensis* Sonn (Sapindaceae), *Dimocarpus longan* Lour. (Sapindaceae), *Mangifera indica* Bl. (Anacardiaceae), *Psidium guajava* L. (Myrtaceae), *Eriobotrya japonica* (Thunb.) Lindl. (Rosaceae), and *Syzygium samarangense* (Bl.) Merr et Perry (Myrtaceae) (Lo & Ho 1989; Ho et al. 1995, 1997; Ho 2004; Yeh et al. 2008). It feeds on leaves using piercing-sucking mouthparts to remove cellular contents, causing yellowish, speckled feeding marks. The mites have a high reproductive potential, and an extremely short life cycle, so they are able to complete numerous generations each growing season (Jian et al. 2016). Consequently, high mite populations infest host plants and reduce yields (Sances et al. 1981). Reportedly, *O. litchii* has become the main pest of *L. chinensis*, *D. longan*, *P. guajava*, *E. japonica*, and *S. samarangense* in Taiwan (Ho 2004). Also it was found recently to cause damage in other litchi-producing areas, such as Guangdong, Hainan, Guangxi, Yunnan, and Fujiang provinces. At present, studies on *O. litchii* are relatively few, and only isolated reports have described its biology, life history, occurrence, damage frequency, and control (Li 2011; Chen et al. 2016).

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Temperature plays an important role on development and reproduction of poikilotherms, such as insects and mites, and it markedly affects the fitness and population dynamics of organisms (Gotoh et al. 2014). Numerous studies indicate that increasing temperature within a certain temperature range enhances mite population growth (Sun et al. 1996); Fu & Zhang 2002; Lin 2013). However, the effects of environmental conditions on the development and reproduction have not been studied in *O. litchii*. In this study, the effects of 5 constant temperatures were determined on development and reproduction under laboratory conditions. This knowledge may prove useful for our understanding of population dynamics of *O. litchii*.

Material and Methods

MITES

The *O. litchii* populations were collected from the litchi variety 'Nuomici' at Dafeng Station of the Plant Protection Research Institute of Guangdong Academy of Agricultural Sciences, Guangzhou, in Mar 2014. *Oligonychus litchii* were reared on fresh litchi var. Nuomici leaves at 26 ± 1 °C, 14:10 h (L:D) photoperiod and 65% RH. Leaves were laid on damp cotton that had been dipped in water to keep the leaves fresh.

EXPERIMENTAL UNITS

The experimental units were maintained using the method of McMurtry and Scriven (1964). *Oligonychus litchii* was placed on the units, which consisted of a Petri dish (90 mm diam) with damp cotton (80 mm diam, 10 mm thick). The leaf was placed on damp cotton, and its margin was wrapped with water-soaked absorbent cotton to prevent escape of *O. litchii*. All mites were transferred to a new experimental unit when the litchi leaves showed signs of deterioration.

IMMATURE DEVELOPMENT AND REPRODUCTION

To obtain synchronized eggs for the experiments, newly laid eggs produced by mated adult females within a 6-h period were removed and placed singly onto each experimental unit. The experimental units with newly laid eggs subsequently were placed in constant-temperature incubators (GXZ380B, Ningbo Jiangnan Instrument Factory, Ningbo, China) at 20, 23, 26, 29, or 32 °C, 65% RH, and a photoperiod of 14:10 h (L:D). Fifty eggs were assigned to each temperature. The experimental units were taken out of the constant temperature incubators, and the leaves were inspected under a binocular microscope (Olympus, SZ4045, Olympus LTD, Shanghai, China) at 50× at 12 h intervals (10:00 AM and 10:00 PM) until they reached maturity. The presence of exuviae was used as the criterion of successful molting to the next development stage. The numbers of eggs, larvae, protonymphs, deutonymphs, males, and females were recorded to prevent overlooking the appearance of mature females. Mature females that had emerged within the last 24 h were transferred singly to a fresh leaf, and supplied with a male to ensure mating. The female and male, constituting a pair, were picked up gently with a soft brush and moved to a fresh leaf disc every d until the female died naturally. The eggs laid on old leaves were counted, and observed continuously to calculate the proportion of *O. litchii* females (females per [females + males]) at maturity.

DEVELOPMENTAL THRESHOLD TEMPERATURE (*C*) AND EFFECTIVE ACCUMULATED TEMPERATURE (*K*)

According to the second expression form of the law of effective accumulated temperature: $T = C + KV$ (Eq. A) (Cai et al. 2011), we can obtain the developmental threshold temperature (°C), effective accumulated temperature (*K*), and correlation coefficient using the linear fitting method. In Equation (A), *T* is temperature, and *V* is the developmental rate, and the value of developmental rate is equal to the reciprocal of developmental duration. The linear regression equation was set to $V = AT + B$ (Eq. B). From this we can obtain the developmental threshold temperature (*C*) and effective accumulated temperature (*K*) from Equations (A) and (B): $C = -B/A$, $K = 1/A$. In our linear regression equation, we set the temperature (*T*) as the independent variable, and the developmental rate (*V*) as the dependent variable. Thus, the value of the developmental threshold was the intercept of the linear equation on the *X* axis, and the value of effective accumulated temperature was the reciprocal of the slope of the equation.

LIFE TABLE PARAMETERS

Life tables were constructed for each temperature based on the records of *O. litchii* development and survival, adult sex ratio, survivorship, and age-specific fecundity (m_x, female progeny per female per d). The life table parameters were estimated from a life-fecundity table according to the equation given by Birch (1948) and Southwood and Henderson (2000):

$$\sum_{i=0}^{n} e^{-r_m x} l_x m_x = 1$$

where *x* is the age class, l_x is the possibility of survival at age *x*, and m_x is the daily number of female offspring at age *x* (Birch 1948). The net reproductive rate R_0 is represented by R_0 =, the intrinsic rate of increase by $r_m = lnR_0/T_0$, the mean generation time T_0 (in d) by $T = lnR_0/r_m$ and the finite rate of increase (λ) by λ =. The doubling time (*DT*) by $DT = ln2/r_m$ was calculated as described by Mackauer (1983). Based on BCaWW method (bias corrected and accelerated bootstrap based on Wyatt and White [1977]), the life history parameters, and 95% confidence limit (CI) were estimated for using 1,000 bootstrap samples (Lawo & Lawo 2011).

STATISTICAL ANALYSIS

The statistical analyses were performed using the SPSS® version 11.5 (IBM Software Group, Somers, New York, USA). The effect of temperature on the developmental period of the *O. litchii* was analyzed using 1-way analysis of variance (ANOVA), and means were separated using Tukey's honest significant difference test (Tukey's HSD test) ($P < 0.05$). The relationship between developmental rate and temperature was measured by linear regression.

Results

DEVELOPMENTAL PERIODS

Durations of the developmental stages of the *O. litchii* at 5 constant temperatures are given in Table 1. As the temperature rose, the development time tended to decline. The egg stage had the longest period of development in the entire period of development, and it decreased significantly with rising constant temperatures. Similar patterns were observed for the larval period, protonymphal period, deutonymphal period, and generation time, but there were no significant differences at 26, 29, and 32 °C. The longest generation time was 34.3 d at 20 °C followed by 21.9 d at 23 °C; the entire generation time was shortest at 32 °C (10.6 d).

Table 1. Developmental periods (d, mean ± SE) of *Oligonychus litchii* at 5 temperatures (65% RH) when reared on litchee.

Temperature (°C)	Egg (d)	Larva (d)	Protonymph (d)	Deutonymph (d)	Generation time (d)
20	11.8 ± 0.2 a	6.7 ± 0.4 a	6.0 ± 0.4 a	6.1 ± 0.4 a	34.3 ± 2.0 a
23	7.8 ± 0.1 b	3.9 ± 0.2 b	3.6 ± 0.5 b	3.7 ± 0.1 b	21.9 ± 0.5 b
26	5.3 ± 0.1 c	2.1 ± 0.1 c	2.0 ± 0.0 c	2.1 ± 0.0 c	13.0 ± 0.2 c
29	4.4 ± 0.0 d	2.0 ± 0.1 c	1.9 ± 0.1 c	1.8 ± 0.1 c	11.2 ± 0.1 d
32	3.8 ± 0.0 e	2.0 ± 0.1 c	1.9 ± 0.1 c	2.2 ± 0.1 c	10.7 ± 0.2 d

Note: Means followed by different lowercase letters within the same column were significantly different ($P < 0.05$; ANOVA and Tukey's HSD test).

DEVELOPMENTAL THRESHOLD TEMPERATURE AND EFFECTIVE ACCUMULATED TEMPERATURE

The linear regression coefficients between developmental rate and temperature for immature stages of the *O. litchii* are shown in Table 2. The developmental rates of the various developmental stages were positively correlated with temperature. The correlation coefficients of the model were over 0.90, which can objectively reflect the relationship between the development rate and temperature of the mites. According to the linear regression equations of the immature stages of *O. litchii*, the developmental threshold temperatures (°C) and accumulated temperatures (degree-d) were: egg (14.3 °C, 66.7 degree-d), larva (14.8 °C, 31.7 degree-d), protonymph (14.1 °C, 31.1 degree-d), deutonymph (13.0 °C, 36.1 degree-d), and entire generation (14.7 °C, 172.4 degree-d) (Table 3).

EFFECTS OF TEMPERATURE ON REPRODUCTION AND ADULT LONGEVITY

As shown in Table 4, the pre-oviposition period, oviposition period, and adult longevity were strongly affected by temperature, and tended to decrease with increasing temperature. The pre-oviposition period, oviposition period, and adult longevity at 20 °C were significantly longer than at any of the other 4 constant temperatures. However, there were no significant differences at 26, 29, and 32 °C. The total fecundity per female (eggs per female) and daily oviposition (eggs per female per d) increased significantly with rising constant temperatures from 20 °C to 26 °C, then decreased gradually with continued rising constant temperatures. The fecundity of *O. litchii* peaked at 26 °C. The lowest daily oviposition was 1.2 eggs at 20 °C. The number of eggs laid by females was similar at 20, 23, and 32 °C.

Age-specific survival rate (l_x) and age-specific fecundity rate (m_x) of *O. litchii* at 5 constant temperatures are shown in Figure 1. The survival curves for the 5 constant temperatures were obviously different. The survival rates of *O. litchii* dropped rapidly with age from larva to deutonymph, and all but 1 stayed at 0.68 and 0.71 for almost 11 d before gradually declining to 0.68 in 20 d, and to 0.00 in 47 d at 26 °C. The first egg-laying was recorded on d 26, 20, 13, 11, and 10 at 20, 23, 26, 29, and 32 °C, respectively (Fig. 1). The peak oviposition age was shortened by increasing temperatures (from 42 d at 20 °C to 13 d at 32 °C), and the peak oviposition rate was about 4 eggs per d at 26 °C.

Table 2. Linear regression models for developmental rate and temperature in the immature stages of *Oligonychus litchii*.

Life stage	Linear model	R^2
Egg	$V = 0.015T - 0.215$	0.997
Larva	$V = 0.032T - 0.468$	0.928
Protonymph	$V = 0.032T - 0.455$	0.942
Deutonymph	$V = 0.028T - 0.360$	0.901
Whole generation	$V = 0.006T - 0.085$	0.970

PARAMETERS OF LIFE TABLE

All major life table parameters are shown in Table 5. The net reproductive rate (R_0) increased significantly from 20 °C (5.05) to 26 °C (37.01), then decreased sharply from 26 °C (37.01) to 32 °C (6.59). Increasing temperatures resulted in shorter mean generation times (T_0) of *O. litchii*, and T_0 was longest at 20 °C (46.28 d) and decreased as temperature increased. The intrinsic rate of increase value (r_m) ranged from 0.04 (at 20 °C) to 0.17 (at 26 and 29 °C). Related to increasing r_m, the finite rates of increase (λ) were all over 1.00, and extended from 20 °C (1.03) to 29 °C (1.19), then decreased at 32 °C (1.13). The population doubling time (*DT*) was longest at 20 °C (19.82 d) and shortest at 29 °C (4.08 d). The proportion of *O. litchii* females (females per [females + males]) at 5 constant temperatures ranged from 0.73 to 0.79, but the influence of the temperatures on the proportion of females (females per [females + males]) was not apparent.

Discussion

Organisms normally have optimal temperatures wherein developmental and reproductive rates are maximized, implying that deviations from optimal conditions would markedly affect the fitness and population dynamics of organisms (Dell et al. 2011; Amarasekare & Sifuentes 2012). This study shows that temperatures have a substantial effect on the development and reproduction of *O. litchii* at 5 constant temperatures. The developmental periods from egg to adult shortened as the temperature increased within certain temperatures (16–29 °C). Similar patterns were observed for the pre-oviposition period, oviposition period, adult longevity, mean generation time (T_0), finite rate of increase (λ), and population doubling time (*DT*), whereas other traits, such as the total fecundity per female (eggs per female), daily oviposition (eggs per female per d) tended to increase significantly with rising constant temperatures from 20 to 26 °C, then declined gradually as the temperatures continuously rose. The total fecundity and daily oviposition peaked at 26 °C, which suggested that the optimum temperature for population increase of *O. litchii* was around 26 °C, and corresponded to

Table 3. Developmental threshold temperature (°C) and effective accumulated temperature (degree-d) for *Oligonychus litchi* at different temperatures.

Stages	Egg	Larva	Protonymph	Deutonymph	Entire generation
Developmental threshold temperature (°C)	14.3	14.8	14.1	13.0	14.7
Effective accumulated temperature (degree-d)	66.7	31.7	31.1	36.1	172.4

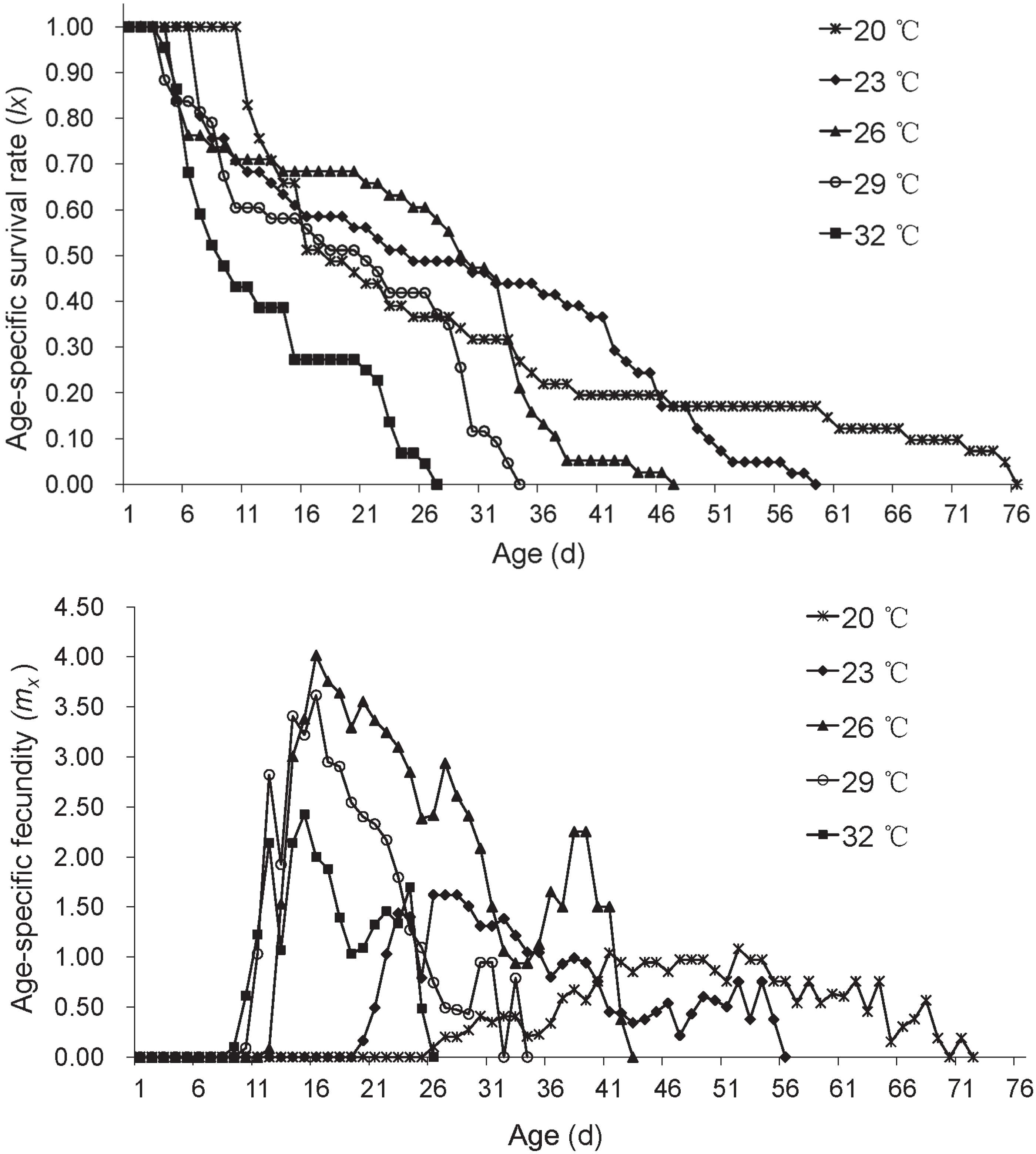

Fig. 1. Age-specific survival rate (l_x) and age-specific fecundity rate (m_x) of adult *Oligonychus litchii* at 5 constant temperatures.

the fecundity pattern of *Oligonychus mangiferus* (Rahman et Punjab) (Acari: Tetranychidae) (Lin 2013). The average temperature from Apr to Oct in South China is about 25 °C, which is beneficial to the development and reproduction of *O. litchii.*

The r_m is an important parameter for describing the growth potential of a population in a given environment because it reflects the overall effects of biotic and abiotic factors on egg eclosion, development, survival, fecundity, etc. (Gabre et al. 2005; Gotoh et

Table 4. Mean number of eggs laid per female, and longevity of adult *Oligonychus litchii* at 5 constant temperatures.

Temperature (°C)	Oviposition per female (eggs per female)	Daily oviposition per female (eggs per female per d)	Pre-oviposition period (d)	Oviposition period (d)	Adult longevity (d)
20	33.0 ± 4.3 c	1.2 ± 0.1 d	4.8 ± 0.4 a	27.4 ± 3.2 a	36.6 ± 3.9 a
23	35.5 ± 2.4 c	1.9 ± 0.1 c	3.3 ± 0.3 b	19.9 ± 1.6 b	26.7 ± 1.6 b
26	77.2 ± 4.1 a	4.1 ± 0.2 a	1.5 ± 0.1 c	19.0 ± 0.9 bc	22.6 ± 1.0 bc
29	48.1 ± 2.8 b	3.3 ± 0.1 b	1.3 ± 0.1 c	14.9 ± 0.9 cd	18.2 ± 0.9 cd
32	33.3 ± 2.2 c	2.9 ± 0.1 b	1.2 ± 0.1 c	11.7 ± 0.5 d	14.3 ± 0.7 d

All data are presented as mean ± standard error (SE). Means followed by different lowercase letter within the same column were significantly different ($P < 0.05$; ANOVA and Tukey's HSD test).

Table 5. Life table parameters of an experimental population of *Oligonychus litchii* at 5 constant temperatures.

Temperature (°C)	Net reproductive rate (R_0)	Mean generation time (T_0)	Intrinsic rate of increase (r_m)	Finite rate of increase (λ)	Population doubling time (*DT*)	Proportion of females (females per [females + males])
20	5.05 ± 0.37 d	46.28 ± 1.86 a	0.04 ± 0.00 d	1.03 ± 0.01 d	19.82 ± 0.31 a	0.76 a
23	11.96 ± 0.54 c	30.93 ± 0.95 b	0.08 ± 0.01 c	1.08 ± 0.00 c	8.64 ± 0.54 b	0.75 a
26	37.01 ± 0.98 a	21.59 ± 0.51 c	0.17 ± 0.01 a	1.18 ± 0.02 a	4.14 ± 0.08 d	0.75 a
29	19.89 ± 0.76 b	17.59 ± 0.22 d	0.17 ± 0.02 a	1.19 ± 0.01 a	4.08 ± 0.11 d	0.79 a
32	6.59 ± 0.25 d	15.70 ± 0.28 e	0.12 ± 0.03 b	1.13 ± 0.01 b	5.77 ± 0.06 c	0.73 a

Means followed by different lowercase letters within the same column were significantly different ($P < 0.05$; BCaWW method).

al. 2014). The r_m values were increased from 20 °C (0.04) to 29 °C (0.17), then decreased at 32 °C (0.12). The finite of rates increase (λ) were over 1.00 at all 5 constant temperatures. These findings were similar to the study of Li et al. (2014), which showed that increasing temperature within a certain temperature range enhanced the population growth for *Eotetranychus kankitus* Ehara (Acari: Tetranychidae). In addition, *O. litchii* is female-biased population wherein females comprise the majority of the population. In many other mites, such as *Tetranychus urticae* Koch (Acari: Tetranychidae) (Ho & Lo 1979), *Panonychus citri* McGregor (Acari: Tetranychidae) (Liu & Horng 1988), and *Oligonychus coffeae* Nietner (Acari: Tetranychidae) (Gotoh & Nagata 2001), the same phenomenon occurs. Previous research has reported that the offspring sex ratio (female:male) of spider mites increases with increasing temperature (Roy et al. 2003). Such a pronounced effect was not observed in our study, although the proportion of *O. litchii* females (females per [females + males]) was increased to 0.79 at 29 °C, there were not significant differences (Table 5).

The linear regression analysis revealed that the developmental threshold temperature from egg to adult was 13.4 °C, which is slightly higher than those found in *Oligonychus uruma* Ehara (Acari: Tetranychidae) (10.5 °C) (Cheng & Cheng 1992), *O. coffeae* (12.5 °C) (Huang 1993), and *O. mangiferus* (11.1 °C) (Fu & Zhang 2002). The effective accumulated temperatures for the entire generation was 172.4 degree-d, which was slightly lower than those found in *O. uruma* (213.7 degree-d) (Cheng & Cheng 1992), *O. coffeae* (212.8 degree-d) (Gotoh & Nagata 2001), and *O. mangiferus* (191.8 degree-d) (Fu & Zhang 2002). The developmental threshold temperatures and effective accumulated temperatures, when combined with years of meteorological data, allows estimation of dates of occurrence and numbers of generations (Sun et al. 1996). Annual effective accumulated temperature in Guangdong Province is around 7,500 degree-d (Huang et al. 2015), suggesting that *O. litchii* could experience 40 generations or more annually. However, organisms are exposed to daily and annually fluctuating temperatures and moistures. The data obtained at constant temperatures are important for determining the potential growth rate of organisms, though the actual growth rates for *O. litchii* will deviate from the predicted values when organisms living in the wild are compared to constant temperatures.

Our study shows that temperature affects the population growth rate of *O. litchii*, and the difference of development and reproduction measured at 5 constant temperatures can be considerable. Additionally, we have shown that the optimum temperature for population increase of *O. litchii* was around 26 °C, although the r_m value and daily oviposition at 26 to 29 °C remained at elevated levels, which may explain the earlier dates of occurrence, increasing heat tolerance, and the population outbreaks of *O. litchii* in the ecosystem under global warming. For better understanding of the effects of environmental conditions on occurrence and damage of *O. litchii*, further research is needed to investigate the impacts of variable temperatures, relative humidity, photoperiods, plant hosts, etc., on population dynamics. Because the interactions between the temperatures, relative humidity, and hosts are likely to be very complex, there is a need for developing a general theoretical framework for linking these 3 aspects of population dynamics.

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