


Impact of constant versus fluctuating temperatures on the development and life history parameters of *Tetranychus urticae* (Acari: Tetranychidae)

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Abstract The impact of daily temperature fluctuations on arthropod life history parameters is inadequately studied compared with the ample amount of research that has been conducted on the effects of constant temperatures. Fluctuating temperatures are likely to be more realistic, as they are ecologically more similar to what these arthropods experience in nature. Here, we compared the impact of 11 constant temperatures that ranged from 10 to 35 °C with fluctuating temperatures with the same corresponding mean temperature and an amplitude of 10 °C between high (12 h) and low (12 h) temperatures on the development and life history parameters of *Tetranychus urticae* under continuous light conditions. No eggs hatched at constant 10 °C, whereas 81.5% of eggs successfully completed development at fluctuating 10 °C (15/5 °C). Egg-to-female adult development was faster under fluctuating temperatures from 12.5 to 27.5 °C than under constant temperatures, whereas the opposite trend was observed at >30 °C. The lower thermal thresholds (T) were 11.63 and 8.63 °C, and thermal constants (K) were 127.81 and 150.69 degree-days for egg-to-female adults at constant and fluctuating temperatures, respectively. The numbers of oviposition days were significantly higher at fluctuating 15 °C than at the corresponding constant temperature, whereas the opposite trend was observed from 20 to 30 °C. The intrinsic rate of increase (r) was higher at fluctuating than at constant 15 °C. The net reproductive rate (R_0) was also higher at fluctuating than at constant 15 and 35 °C, but showed an opposite trend at 20 and 25 °C. We conclude that fluctuating temperatures should be considered to accurately predict spider mite population dynamics in nature.

Keywords Spider mites · Lower thermal threshold · Thermal biology · Degree-day · Population dynamics

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Introduction

An effective approach to predicting the effect of environmental changes on arthropods is to describe how temperature affects population dynamics based on its effects on individuals. Temperature is known as the most important abiotic factor that affects arthropod development rates, life history parameters and distribution (Blanford et al. 2013; Paaajmans et al. 2013); it directly affects the dynamics of populations by affecting the birth, death and growth rates of individuals. With regards to pest management approaches, understanding the basic thermal biology of insect pests is important for predicting and managing pest outbreaks (Luedeling et al. 2011; Haavik et al. 2013).

Lower thermal thresholds, thermal constants and intrinsic rates of increase are important parameters for forecasting insect growth in nature. As temperature regimes affect development and other life history parameters, diurnal temperature ranges should be considered to measure such parameters (Blanford et al. 2013; Paaajmans et al. 2013; Ullah and Lim 2015). Ongoing changes in climate alter mean temperature and impact daily temperature fluctuations (Zhou et al. 2009). The number of generations of various arthropods, including mites from the family Tetranychidae, has increased because of climate change (Luedeling et al. 2011). The two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), is one of the most devastating polyphagous herbivores, because it feeds on over 1100 plant species in more than 140 plant families that produce a broad spectrum of chemical defenses (Migeon and Dorkeld 2006–2017).

Basic information about the development and life table parameters of *T. urticae* under constant temperatures have been studied (Riahi et al. 2013). However, constant temperatures in the laboratory may not accurately reflect the ecological responses of insects and mites in nature. Ectotherms such as *T. urticae* are more sensitive to temperature fluctuation, because they experience this variation in nature. Several studies have reported the effect of fluctuating temperatures on development and life history parameters of *T. urticae* (Vangansbeke et al. 2013, 2015; Gotoh et al. 2014). However, the mechanism behind differences in development rate under fluctuating compared with constant temperatures has been less investigated (Liu et al. 1995). Understanding the effect of fluctuating temperatures on the survival, development and reproduction of *T. urticae* is crucial for forecasting, managing and utilizing of this pest. Development rates can greatly differ for *T. urticae* reared at constant or fluctuating temperatures, and larger temperature fluctuations yield larger differences (Gotoh et al. 2014). However, development rate has not been studied under a wide range of fluctuating temperatures, although such data are necessary to explain population fluctuations under natural conditions.

For a wide range of temperatures, we used mean temperatures that fluctuated at an amplitude of 10 °C between high (12 h) and low (12 h) temperatures for comparison with constant temperatures. The purpose of this study was to investigate the effects of constant and fluctuating temperatures on development and survival of the immature stages of *T. urticae*, as well as the effects of temperature on demographic parameters (adult survival, longevity, fecundity and intrinsic rate of increase) under laboratory conditions. This information will provide a foundation for evaluating pest management strategies and analyzing population dynamics.

Materials and methods

Spider mite culture

Two-spotted spider mite, *T. urticae*, was originally collected from strawberry, *Fragaria × ananassa* Duchesne, in Tokoro, Hokkaido, Japan, on 30 May 2014. Laboratory stocks were maintained on leaf discs (16 cm²) of common bean (*Phaseolus vulgaris* L.), placed on water-saturated polyurethane mats in plastic dishes (9 cm diameter, 2 cm depth) and kept at 25 ± 1 °C and 60–70% RH under a 16:8 h L:D photoperiod. The edges of bean leaves were covered with moist tissue paper to provide free water and prevent mites from escaping. The leaves were replaced whenever they appeared to be dried out or overexploited by feeding spider mites.

Experimental set-up

The experiments consisted of 11 constant temperatures and 11 fluctuating temperatures, that is 11 pairs of a high and a low temperature—these pairs differed 10 °C and had the same mean as the 11 constant temperatures. Constant temperatures were 10 to 35 °C at 2.5 °C intervals (viz. 10, 12.5, 15, 17.5, 20, 22.5, 25, 27.5, 30, 32.5 and 35 °C). Fluctuating temperatures consisted of a 12-h warm phase and 12-h cool phase, with an amplitude of 10 °C between the high and low temperatures (Fig. 1) (T/C = 15/5 °C, 17.5/7.5 °C, 20/10 °C, 22.5/12.5 °C, 25/15 °C, 27.5/17.5 °C, 30/20 °C, 32.5/22.5 °C, 35/25 °C, 37.5/27.5 °C and 40/30 °C). A 24:0 h L:D photoperiod was used to prevent diapause induction of female *T. urticae*. The fluctuating temperatures were performed using two incubators of the same type (MIR-554, Panasonic Co., Osaka, Japan).

Immature development

A total of 125–130 adult females that had already mated were obtained from mite cultures at each temperature. They were individually transferred onto a leaf discs (0.5 cm diameter) of common bean. These leaf discs were transferred to an incubator with the set temperature regimes to be tested, and each leaf disc was considered a replicate. Females were allowed to lay eggs for 24 h, but eggs laid during this period were discarded to avoid the effect of

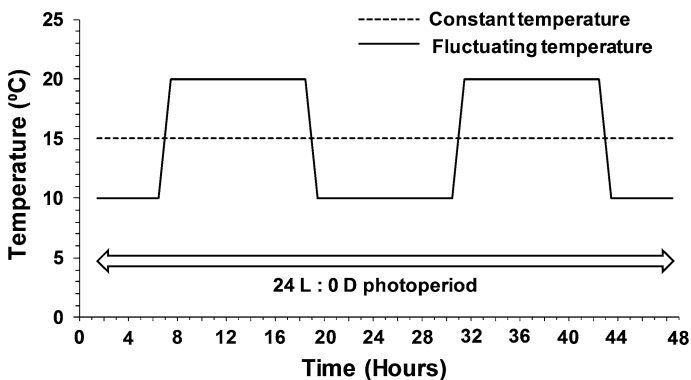


Fig. 1 Simulated scheme for temperature transition and photoperiodic regimes during the experiments (i.e., at a 15 °C constant temperature and an amplitude of 10 °C for fluctuating temperatures)

25 °C rearing environment. Subsequently, females were allowed to lay eggs on the leaf discs for 24 h at average mean temperatures of 10–22.5 °C and 12 h at average mean temperatures of 25–35 °C; then, the female was removed from the arena. Eggs produced by females were reduced to one on each leaf disc by destroying all but one egg with a needle. Each individual was observed with a stereoscopic microscope (SZ40, Olympus Corporation, Tokyo, Japan) to record the development time until all individuals reached adulthood.

Observation was done every 24 h for constant temperatures that ranged from 10 to 22.5 °C and fluctuating temperatures that ranged from 15/5 °C to 27.5/17.5 °C. However, observation was done every 12 h for constant temperatures that ranged from 25 to 35 °C and fluctuating temperatures that ranged from 30/20 °C to 40/30 °C. The sex of all individuals was identified during the teleiochrysalis stage, the last immature quiescent stage. When female *T. urticae* reached the teleiochrysalis stage, they were paired with adult males. If not enough males were available, male adults from the mass-rearing colony were used, but they were excluded from life table analysis. A male was kept on the disc for the total experimental period. If a male died before the female, a new male adult was recruited from the mass-rearing colony, but this male was excluded from life table analysis.

Reproduction and adult longevity

Newly emerged females obtained from the five previous constant temperature regimes (15, 20, 25, 30 and 35 °C) and six fluctuating temperature regimes ($T/C = 15/5$ °C, $20/10$ °C, $25/15$ °C, $30/20$ °C, $35/25$ °C and $40/30$ °C) were used to assess reproduction and adult longevity. The leaf discs were observed at the same interval as above (24 or 12 h) to determine the fecundity. The number of eggs laid by each female was recorded under a stereomicroscope until all mites had died. Because viable eggs are essential for estimating demographic parameters (Mou et al. 2015), eggs laid by individual females were kept until hatching to confirm that they were viable.

Development rate model

Development rates (calculated as $1/\text{development time}$) at different temperatures were used in a linear model. The lower thermal thresholds and thermal constants of *T. urticae* at both constant and fluctuating temperatures were determined using Campbell's (1974) method:

$$K = (T - T_0)D,$$

where D , T , T_0 and K represent the total preadult duration (days), temperature (°C), lower developmental threshold and thermal summation, respectively. The thermal summation K and lower developmental threshold T_0 were estimated based on the following linear regression model:

$$\frac{1}{D} = -\frac{T_0}{K} + \frac{1}{K}T.$$

Demographic parameters

The life history of individuals in each temperature was analyzed using TWOSEX-MSChart (Chi 2017), based on age-stage two-sex life table (Chi and Liu 1985) and the

method described by Chi (1988). The age-stage specific survival rate (s_{xj}), age-specific survival rate (l_x), age-specific fecundity (m_x) and age-stage specific fecundity (f_{xj}) were calculated using methods developed by Chi and Liu (1985). The net reproductive rate (R_0) is the total number of offspring that an individual can produce during its lifetime (Tuan et al. 2016) and was calculated as follows:

$$R_0 = \sum_{x=0}^{\infty} (l_x m_x).$$

The intrinsic rate of increase (r) was calculated using the Lotka–Euler equation with age indexed from zero (Tuan et al. 2016) as follows:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} (l_x m_x) = 1,$$

where x is female age in days, l_x is the age-specific survival rate [(fraction of females surviving at age x) \times (rate of egg hatchability) \times (survival rate of immature stages)] and m_x is the expected number of daughters produced per female alive at age x [(age-specific oviposition) \times (proportion of females)]. The proportion of females was calculated from the F_1 generation (see Table 1). The mean generation time (T) represents the amount of time that a population requires to increase its size to R_0 -fold as time approaches infinity and the population settles to a stable age-stage distribution (Tuan et al. 2016). Mean generation time was calculated as follows:

$$T = \frac{\ln R_0}{r}.$$

The finite rate of increase (λ) is a multiplication factor of the original population at each time period. The finite rate of increase was calculated as follows:

$$\lambda = e^r.$$

The age-stage life expectancy (e_{xj}) is the time length that an individual of age x and stage j is expected to survive and it was calculated as follows:

$$e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^k S'_{iy},$$

where S'_{iy} is the probability that an individual of age x and stage j will survive to age i and stage y , and was calculated by assuming $S'_{iy} = 1$, following the procedure described in Chi (1988).

The age-stage reproductive value (v_{xj}) is defined as the contribution of n individuals of age x and stage j to the future population. Based on Tuan et al. (2016), the reproductive value (v_{xj}) in the age-stage, two-sex life table was calculated as follows:

$$v_{xj} = \frac{e^{y(x+1)}}{S_{xj}} \sum_{i=x}^{\infty} e^{-r(i+1)} \sum_{y=j}^k S'_{iy} f_{iy}.$$

where f_{iy} is the probability that an individual of age x and stage j will reproduce to age i and stage y . The variances and standard errors of the population parameters were estimated by bootstrapping (Efron and Tibshirani 1993) with 100,000 replicates to obtain

stable estimates (Akca et al. 2015). Then, we performed the paired bootstrap test to examine the impacts of different temperature treatments on life history parameters.

Polynomial regression models with first, second and, in some cases, third order terms of constant and fluctuating temperatures as predictor variables of r and R_0 were fitted to data for each condition separately.

Results

Immature development

Both male and female *T. urticae* successfully completed their development from egg-to-adult under constant and fluctuating temperatures that ranged from 10 to 35 °C, except at constant 10 °C (Table 1). No *T. urticae* eggs (0/100) hatched at constant 10 °C. The immature survival rate was significantly higher under fluctuating temperatures when compared with the corresponding constant temperatures below 17.5 °C ($P < 0.05$). However, no significant differences were observed at temperatures of 20 °C and higher ($P > 0.05$, Table 1).

Egg-to-adult development time decreased with increasing temperature up to 35 °C under constant and fluctuating conditions. Egg-to-adult female development time was shorter at fluctuating than constant temperatures when individuals were reared at 12.5, 15, 17.5, 20, 22.5, 25 and 27.5 °C ($P < 0.05$). However, there were no significant differences at 30 °C ($P > 0.05$), and opposite trends at other temperatures ($P < 0.05$, Table 1). Under both temperature conditions, males tended to develop more rapidly than females (Table 1).

Lower thermal thresholds and thermal constants

Development rates for the 12.5 to 35 °C range of constant temperatures (no eggs hatched at 10 °C) and 10 to 35 °C range of fluctuating temperatures for egg-to-adult female and egg-to-adult male were fit well to the linear model (constant: $0.9871 \leq R^2 \leq 0.9936$; fluctuating: $0.9728 \leq R^2 \leq 0.9776$). The estimated lower thermal thresholds (T) for egg-to-female adults were 11.63 °C at constant temperatures and 8.63 °C at fluctuating temperatures ($P < 0.001$). The thermal constants (K) for egg-to-female adults were estimated as 127.81 degree-days (DD) and 150.69 DD at the respective temperature conditions ($P = 0.008$). The estimated lower thermal thresholds for egg-to-male adults were 11.52 °C at constant temperatures and 8.93 °C at fluctuating temperatures ($P < 0.001$). The thermal constants (K) for egg-to-male adults were estimated as 127.14 and 142.13 DD at the respective temperature conditions ($P < 0.001$).

Reproduction and adult longevity

Adult preoviposition period and total pre-oviposition period decreased with increasing temperature up to 35 °C for both conditions (Table 2). Fecundity was higher at fluctuating temperatures than at constant temperatures when reared at 15 and 35 °C, whereas the opposite trend was observed at 20 and 25 °C. Oviposition period (days) was also decreased with increasing temperature up to 35 °C for both conditions (Table 2). Oviposition period at fluctuating 15 °C showed longer duration than at 25 and 30 °C, it was twice as long as at fluctuating 25 °C and thrice as at fluctuating 30 °C, which might result in the highest

Table 1 Mean (± SE) developmental duration (days) from egg-to-adult and survival rate (%) of *Tetranychus urticae* on bean leaf discs at constant and fluctuating temperatures (12 h thermophase and 12 h cryophase) under a 24:0 h L:D photoperiod

Temperature (°C)	N	Egg	Larva	Protonymph	Deutonymph	Egg-to-adult	% Immature survival
Constant							
10	♀	-	-	-	-	-	0.0 [100] ^a
	♂	-	-	-	-	-	
12.5	♀	28.8 ± 0.35Ab	11.6 ± 0.25Aa	9.5 ± 0.19Aa	11.7 ± 0.20Aa	61.5 ± 0.63Aa	36.2 [130]B
	♂	30.7 ± 0.43Aa	12.2 ± 0.49Aa	9.1 ± 0.27Aa	10.2 ± 0.19Ab	62.2 ± 0.95Aa	
15	♀	16.8 ± 0.10Af	6.4 ± 0.08Ade	5.5 ± 0.06Ad	7.2 ± 0.11Acde	35.9 ± 0.17Ad	69.2 [130]B
	♂	16.7 ± 0.14Af	5.9 ± 0.17Ae	5.3 ± 0.13Ad	6.5 ± 0.11Ae	34.3 ± 0.29Ae	
17.5	♀	11.4 ± 0.08Ah	4.6 ± 0.07Afg	3.8 ± 0.06Af	5.1 ± 0.11Afg	25.0 ± 0.16Ah	79.2 [130]B
	♂	12.2 ± 0.08Ag	4.1 ± 0.05Ah	3.8 ± 0.06Af	4.4 ± 0.11Ahi	24.5 ± 0.18Ah	
20	♀	7.6 ± 0.05Ak	2.9 ± 0.05Ajk	2.4 ± 0.06Ah	3.2 ± 0.05Ajk	16.2 ± 0.05Aj	88.8 [125]A
	♂	7.7 ± 0.08Ak	3.1 ± 0.15Ajk	2.2 ± 0.10Abij	2.7 ± 0.09Al	15.7 ± 0.17Ajk	
22.5	♀	5.2 ± 0.05Bn	2.3 ± 0.06Amn	2.0 ± 0.02Aij	2.7 ± 0.06Alm	12.2 ± 0.07Am	92.3 [130]A
	♂	5.6 ± 0.07Am	2.2 ± 0.07Ano	2.0 ± 0.05Aij	2.1 ± 0.07Ano	11.9 ± 0.09Amn	
25	♀	4.6 ± 0.03Ao	1.9 ± 0.03Aop	1.7 ± 0.03Ak	2.2 ± 0.03Ano	10.4 ± 0.05Ao	89.2 [130]A
	♂	4.8 ± 0.05Ao	1.8 ± 0.04Apo	1.5 ± 0.02Ak	1.9 ± 0.03Aop	10.0 ± 0.06Ao	
27.5	♀	3.9 ± 0.03Ap	1.4 ± 0.02Brs	1.3 ± 0.03Alm	2.0 ± 0.02Aop	8.4 ± 0.03Aqr	93.1 [130]A
	♂	4.0 ± 0.02Ap	1.4 ± 0.05Arst	1.2 ± 0.04Almmo	1.6 ± 0.03Aqr	8.1 ± 0.06Ar	
30	♀	3.0 ± 0.03Astu	1.2 ± 0.03Auv	1.0 ± 0.01Aopq	1.4 ± 0.03Arst	6.4 ± 0.03Au	84.0 [125]A
	♂	3.0 ± 0.06Arst	1.2 ± 0.05Auv	1.2 ± 0.05Almn	1.3 ± 0.08Astuv	6.7 ± 0.11At	
32.5	♀	2.7 ± 0.03Au	1.1 ± 0.03Auv	0.9 ± 0.02Bpq	1.2 ± 0.03Atuvw	6.1 ± 0.04Bvwx	90.8 [130]A
	♂	3.0 ± 0.02Arst	1.0 ± 0.02Bv	0.9 ± 0.03Aq	1.0 ± 0.03Bwx	5.9 ± 0.03Bx	
35	♀	2.1 ± 0.02Bx	1.3 ± 0.03Astu	1.0 ± 0.02Aopq	1.0 ± 0.03Bwx	5.5 ± 0.04By	88.0 [125]A
	♂	2.4 ± 0.05Bw	1.1 ± 0.05Av	1.1 ± 0.04Aopq	0.9 ± 0.04Bx	5.4 ± 0.06Ay	

Table 1 continued

Temperature (°C)	N	Egg	Larva	Protonymph	Deutonymph	Egg-to-adult	% Immature survival
Fluctuating ^b							
15/5 (10)	♀ 67	21.3 ± 0.16d	9.3 ± 0.17b	7.6 ± 0.08b	9.2 ± 0.17b	45.9 ± 0.49b	81.5 [130]
	♂ 39	22.8 ± 0.23c	8.9 ± 0.24b	7.6 ± 0.33b	7.9 ± 0.23c	47.3 ± 0.80b	
17.5/7.5 (12.5)	♀ 68	16.4 ± 0.07Bf	7.7 ± 0.09Bc	6.2 ± 0.07Bc	7.4 ± 0.06Bcd	37.4 ± 0.19Bc	80.8 [130]A
	♂ 37	17.7 ± 0.10Be	6.7 ± 0.08Bd	5.7 ± 0.08Bcd	6.5 ± 0.09Bde	36.9 ± 0.26Bcd	
20/10 (15)	♀ 80	12.2 ± 0.05Bg	5.0 ± 0.06Bf	4.5 ± 0.06Be	5.5 ± 0.07Bf	27.3 ± 0.19Bf	88.5 [130]A
	♂ 35	12.7 ± 0.08Bg	4.4 ± 0.09Bgh	4.1 ± 0.09Bef	4.7 ± 0.10Bgh	25.9 ± 0.10Bg	
22.5/12.5 (17.5)	♀ 58	9.0 ± 0.04Bj	3.4 ± 0.07Bi	3.3 ± 0.06Bg	4.0 ± 0.04Bi	19.6 ± 0.17Bi	92.3 [130]A
	♂ 62	9.6 ± 0.06Bi	3.2 ± 0.05Bij	3.1 ± 0.05Bg	3.4 ± 0.07Bj	19.1 ± 0.13Bi	
25/15 (20)	♀ 86	7.1 ± 0.05Bi	2.5 ± 0.05Blm	2.5 ± 0.05Ah	3.2 ± 0.05Ajk	15.2 ± 0.11Bkl	93.6 [125]A
	♂ 31	7.2 ± 0.13Bl	2.7 ± 0.13Akl	2.3 ± 0.14Ahi	2.9 ± 0.10Akl	15.2 ± 0.26Bl	
27.5/17.5 (22.5)	♀ 64	5.5 ± 0.06Amn	2.0 ± 0.04Bnop	2.0 ± 0.03Aij	2.3 ± 0.06Bmn	11.9 ± 0.10Bmn	96.2 [130]A
	♂ 61	5.6 ± 0.07Am	2.0 ± 0.06Bop	2.0 ± 0.06Aj	1.9 ± 0.06Bop	11.6 ± 0.15Bn	
30/20 (25)	♀ 70	4.0 ± 0.01Bp	1.8 ± 0.03Bp	1.3 ± 0.04Blm	1.7 ± 0.05Bop	9.0 ± 0.01Bp	92.8 [125]A
	♂ 46	4.1 ± 0.03Bp	1.6 ± 0.05Bqr	1.3 ± 0.04Bl	1.7 ± 0.05Bpq	8.8 ± 0.07Bq	
32.5/22.5 (27.5)	♀ 76	3.1 ± 0.03Br	1.6 ± 0.03Aqr	1.3 ± 0.03Alm	1.4 ± 0.04Bstu	7.3 ± 0.09Bs	91.5 [130]A
	♂ 43	3.4 ± 0.05Bq	1.4 ± 0.05Ais	1.2 ± 0.04Almmo	1.3 ± 0.05Bstu	7.1 ± 0.05Bs	
35/25 (30)	♀ 82	2.9 ± 0.02Brst	1.1 ± 0.02Buv	1.0 ± 0.02Aopq	1.4 ± 0.04Arst	6.4 ± 0.10Atu	91.5 [130]A
	♂ 37	3.0 ± 0.02Ais	1.1 ± 0.03Auv	1.0 ± 0.03Bopq	1.2 ± 0.05Auvw	6.2 ± 0.08Buv	
37.5/27.5 (32.5)	♀ 56	2.7 ± 0.03Au	1.2 ± 0.03Auv	1.1 ± 0.03Amnop	1.2 ± 0.03Atuv	6.3 ± 0.06Au	83.8 [130]A
	♂ 53	3.0 ± 0.04Arst	1.1 ± 0.03Auv	1.0 ± 0.02Apq	1.2 ± 0.04Atuvw	6.1 ± 0.05Auvw	
40/30 (35)	♀ 71	2.5 ± 0.01Av	1.0 ± 0.01Bv	1.0 ± 0.01Aopq	1.5 ± 0.02Aqrs	6.0 ± 0.01Awx	80.8 [130]A
	♂ 34	2.8 ± 0.04Atu	0.8 ± 0.04Bw	0.9 ± 0.04Bq	1.1 ± 0.03Avw	5.5 ± 0.03Ay	

^a Numeral in bracket indicates the number of eggs tested

^b Mean temperature in parentheses

N Number of individuals tested

Different upper case letters following means within a column denote significant differences between constant and fluctuating condition at the same (mean) temperature, whereas different lower case letters following means denote significant differences among temperatures based on the paired bootstrap test ($P < 0.05$)

Table 2 Mean (\pm S.E.) duration (days) of adult phases; adult preoviposition period (APOP), total pre-oviposition period (TPOP), fecundity (total number of eggs laid), oviposition days and longevity of *Tetranychus urticae* on bean leaf discs at constant and fluctuating temperatures under a 24:0 h L:D photoperiod

Temperature (°C)	APOP	TPOP	Fecundity	Oviposition days	Longevity of female	Longevity of male
Constant						
15	5.5 \pm 0.15Aa	41.4 \pm 0.22Ab	65.6 \pm 5.42Bde	22.6 \pm 1.39Bb	67.6 \pm 1.55Ab	74.6 \pm 2.34Aa
20	1.9 \pm 0.07Ac	18.0 \pm 0.07Ad	139.68 \pm 8.62Abc	17.6 \pm 0.84Ac	38.1 \pm 1.09Ac	41.2 \pm 0.56Ac
25	0.7 \pm 0.03Ad	11.0 \pm 0.06Af	167.99 \pm 7.41Aa	7.3 \pm 0.24Ad	28.3 \pm 0.61Ad	23.0 \pm 0.43Ad
30	0.4 \pm 0.03Ae	6.7 \pm 0.05Ah	68.9 \pm 3.98Acd	3.4 \pm 0.13Af	13.8 \pm 0.28Af	13.0 \pm 0.33Af
35	0.2 \pm 0.03Af	5.6 \pm 0.04Bj	26.4 \pm 1.96Bf	2.2 \pm 0.08Bg	9.9 \pm 0.21Bh	5.3 \pm 0.14Bf
Fluctuating^a						
15/5 (10)	6.4 \pm 0.27a	53.9 \pm 0.50a	30.5 \pm 3.74f	17.0 \pm 1.66c	79.9 \pm 2.02a	83.2 \pm 1.80a
20/10 (15)	3.3 \pm 0.07Bb	30.5 \pm 0.09Bc	162.2 \pm 6.42Aab	29.3 \pm 1.00Aa	67.2 \pm 1.29Ab	64.8 \pm 1.25Bb
25/15 (20)	1.7 \pm 0.06Bc	17.0 \pm 0.08Be	85.9 \pm 6.48Bd	12.4 \pm 0.63Bc	31.3 \pm 0.70Bd	39.4 \pm 0.98Ac
30/20 (25)	0.7 \pm 0.05Ad	9.6 \pm 0.05Bg	77.4 \pm 5.11Bcd	4.7 \pm 0.23Be	19.3 \pm 0.50Be	17.3 \pm 0.51Be
35/25 (30)	0.2 \pm 0.03Af	6.7 \pm 0.05Ah	64.4 \pm 2.93Acd	3.2 \pm 0.09Bf	12.9 \pm 0.20Bf	12.5 \pm 0.24Af
40/30 (35)	0.2 \pm 0.03Af	6.2 \pm 0.03Ai	42.2 \pm 3.34Ae	2.5 \pm 0.09Afg	11.2 \pm 0.20Afg	16.9 \pm 0.37Ac

^a Mean temperature in parentheses

Different upper case letters following means within a column denote significant differences between constant and fluctuating condition at the same (mean) temperature, whereas different lower case letters following means denote significant differences among temperatures based on the paired bootstrap test ($P < 0.05$)

fecundity at fluctuating 15 °C. In general, the longevity decreased with increasing temperature in both constant and fluctuating conditions (Table 2). Longevity was higher for females at fluctuating 35 °C than at the corresponding constant temperature, whereas the opposite trend was observed at 20, 25 and 30 °C (Table 2). Male longevity was higher at constant 15 and 25 °C than at the corresponding fluctuating temperatures, whereas the opposite trend was observed at 35 °C (Table 2).

Demographic parameters

The age-stage survival rate curves (S_{xj}) illustrate the probability that a newly emerged *T. urticae* individuals will survive to age x and stage j . For constant temperatures, the curves for different stages and sexes are shown in Fig. 2 (left and right panels, respectively). Similar data are shown for fluctuating temperatures in Fig. 3. In general, the age-stage survival rates of *T. urticae* differed between constant and fluctuating temperatures.

The age-specific survival rate (l_x), age-specific fecundity (m_x), age-specific maternity ($l_x m_x$) and age-stage-specific fecundity (f_{xj}) for each temperature treatment are presented in Figs. 4 and 5. The age-specific survivability (l_x) decreased with increasing mean temperatures of both constant and fluctuating temperatures that ranged from 15 to 35 °C. The oviposition period decreased with increasing temperature for *T. urticae* under both conditions. *Tetranychus urticae* took longer to reach peak m_x as the temperature decreased under constant conditions (Fig. 4). A similar response was also shown in fluctuating temperatures (Fig. 5). Net maternity values ($l_x m_x$) were lower at higher temperatures because of the low survival rate, although peak values were higher at 25 °C (8.18 eggs under constant and 6.00 eggs under fluctuating temperatures) and 30 °C (7.47 eggs under constant and 9.19 eggs under fluctuating temperatures) than at 15 °C (1.49 eggs under constant and 3.80 eggs under fluctuating temperatures) (Figs. 4, 5).

The e_{xj} of each age-stage group of *T. urticae* under constant (Fig. 6, left panels) and fluctuating temperatures (Fig. 7, left panels) showed the length of time that individuals of age x and stage j were expected to live after age x under different temperature conditions. The peak life expectancy (e_{xj}) of adult females reared under constant conditions decreased with increasing temperature (Fig. 6, right panels). A similar response was observed for adult female *T. urticae* at fluctuating temperatures (Fig. 7, right panels).

Reproductive value is defined as the contribution of an individual to the future population (Fisher 1930). The reproductive values (v_{xj}) of *T. urticae* individuals reared under constant and fluctuating conditions at age x and stage j are presented in Figs. 8 and 9. The effect of age on the reproductive value can be clearly observed in the v_{xj} curves. The peak v_{xj} of an adult female was 31.76, 50.42, 74.47, 41.07 and 20.18 day⁻¹ at constant 15, 20, 25, 30 and 35 °C, respectively (Fig. 8, right panels), and the peak v_{xj} of an adult female was 51.86, 37.01, 42.52, 39.10 and 29.63 day⁻¹ at the respective fluctuating temperatures (Fig. 9, right panels).

The net reproductive rate (R_0), intrinsic rate of increase (r), finite rate of increase (λ) and mean generation time (T) were significantly affected by constant and fluctuating temperatures (Table 3). At fluctuating 10 °C, the R_0 , r and T values were 15.69 ± 2.34 , 0.0402 ± 0.0020 day⁻¹ and 68.49 ± 0.92 days, respectively. The R_0 values were higher at fluctuating temperatures than the corresponding constant temperatures of 15 and 35 °C, but they showed an opposite trend at 20 and 25 °C, and did not significantly differ at 30 °C ($P < 0.05$) (Fig. 10; Table 3). The r and λ values were higher at fluctuating temperatures with a mean of 15 °C than those at the corresponding constant temperature. The peak values of r were 0.423 and 0.438 day⁻¹ under both constant and fluctuating conditions at

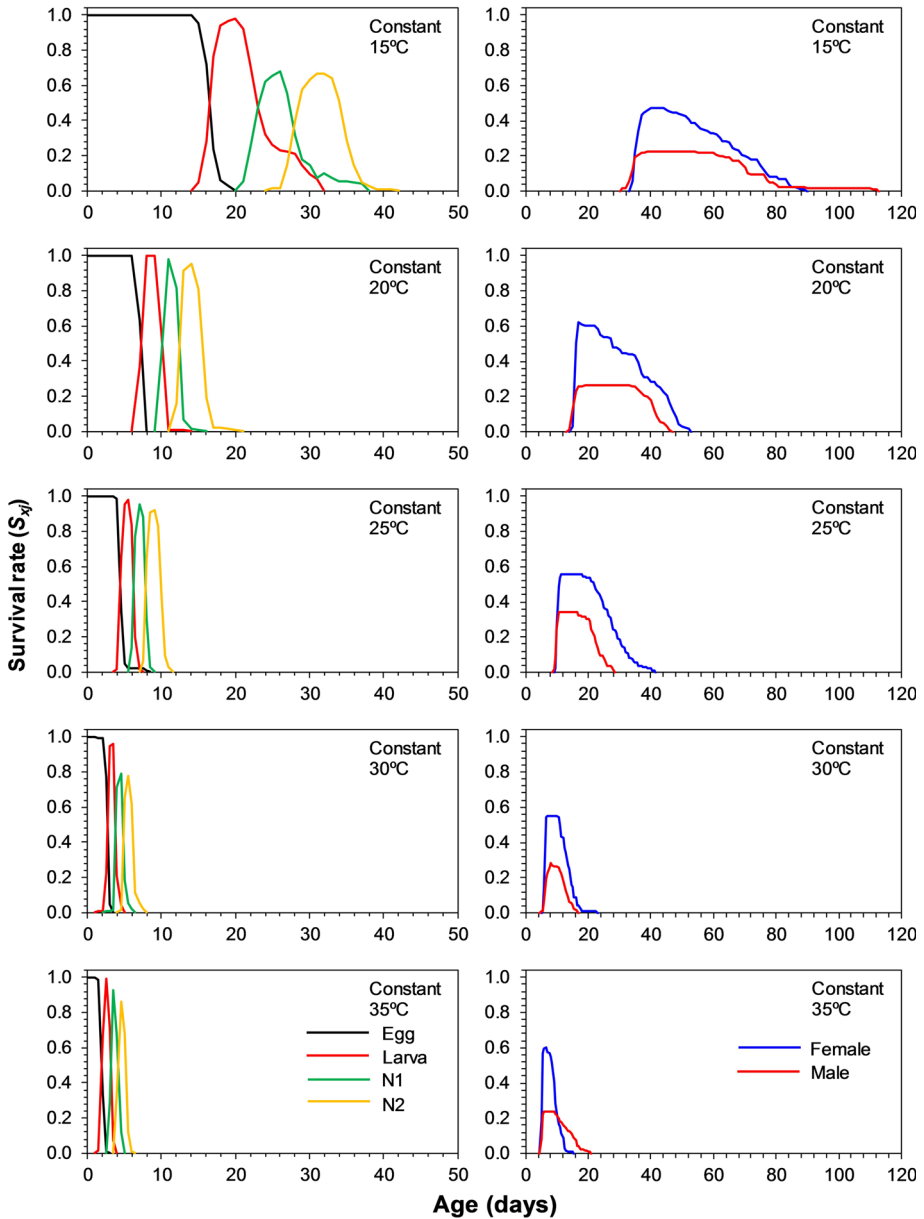


Fig. 2 Age-stage survival rate (S_{xj}) of *Tetranychus urticae* at five constant temperatures. *Left panels* depict different life stages and *right panels* depict different adult sexes. S_{xj} depicts the probability that a newborn will survive to age x and stage j . The variable developmental rates among individuals overlap between different stages during developmental periods

30 °C, respectively (Fig. 10; Table 3). The peak values of λ were 1.526 and 1.550 day⁻¹ at constant and fluctuating conditions of 30 °C, respectively. Mean generation times varied from 7.07 to 54.12 days at constant temperatures from 15 to 35 °C and from 8.00 to

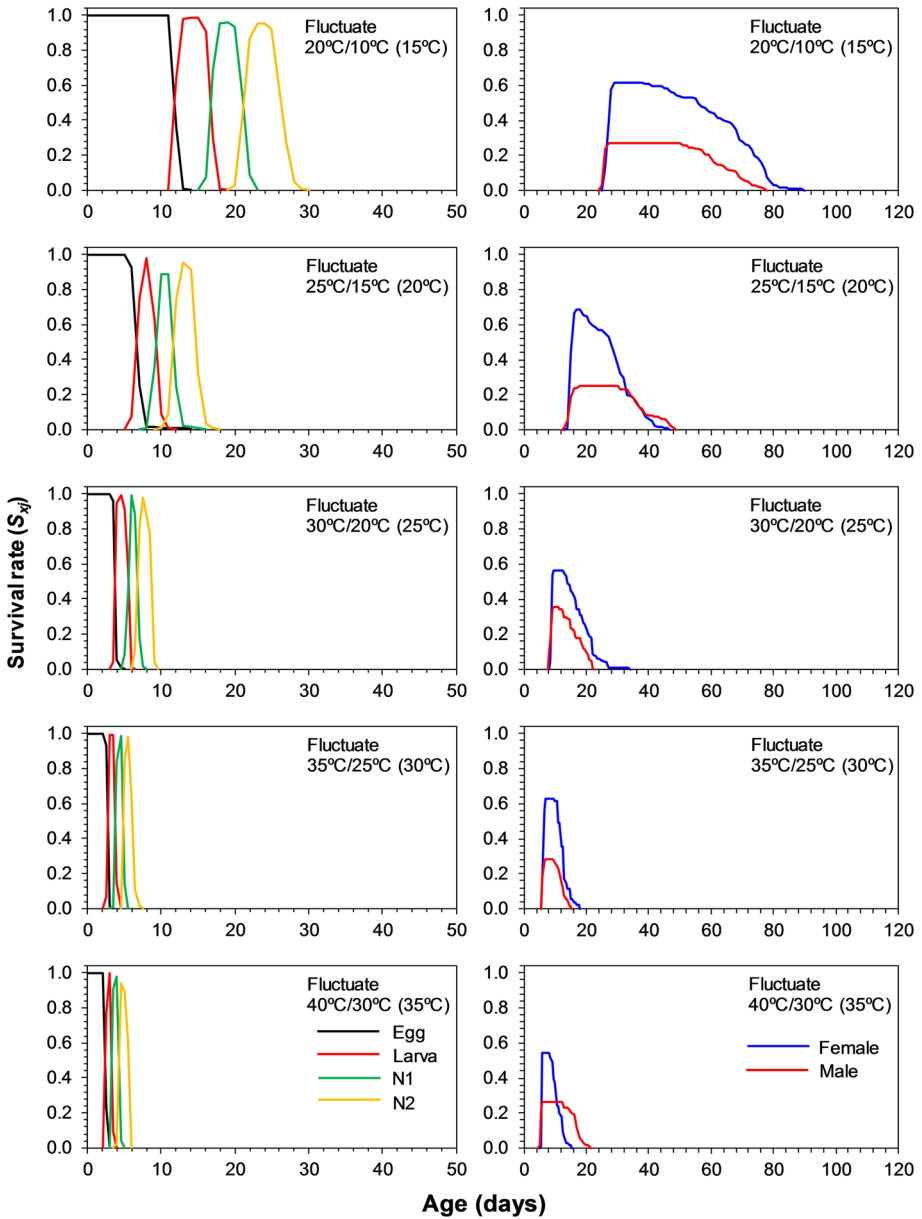


Fig. 3 Age-stage survival rate (S_{xj}) of *Tetranychus urticae* at five fluctuating temperatures. *Left panels* depict different life stages and *right panels* depict different adult sexes. S_{xj} depicts the probability that a newborn will survive to age x and stage j . The variable developmental rates among individuals overlap between different stages during developmental periods

44.32 days at the corresponding fluctuating temperatures (Table 3). The mean generation time was higher under constant than under fluctuating temperatures at a range of 15 to 30 °C; at 35 °C, it was longer at fluctuating temperatures (8.00 days) than at the corresponding constant temperature (7.07 days).

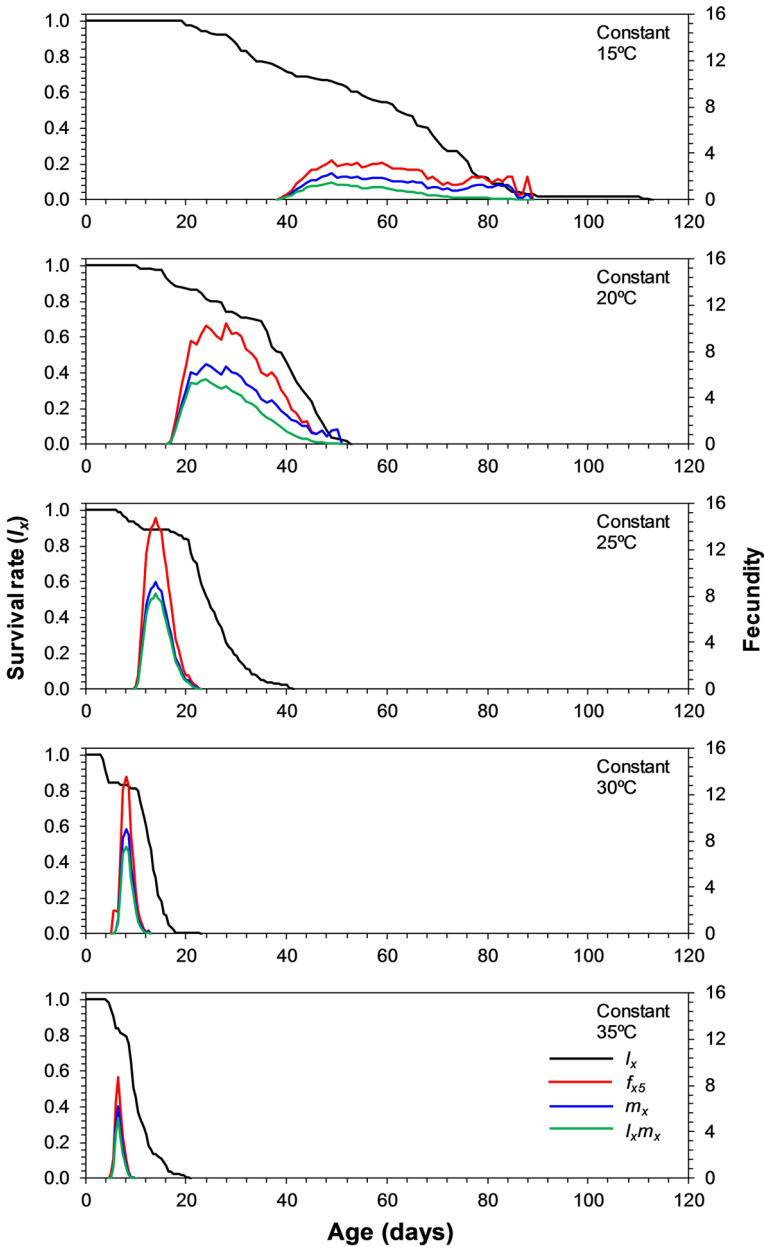


Fig. 4 Age-specific survival rate (l_x), fecundity (m_x), maternity ($l_x m_x$) and age-stage-specific fecundity ($f_{x,s}$) of *Tetranychus urticae* at five constant temperatures

Discussion

Temperature fluctuations had a substantial impact on the egg-to-adult development rates of *T. urticae* compared with the corresponding constant temperatures. Compared with earlier studies on thermal responses of arthropods (Fantinou et al. 2003), development rates were

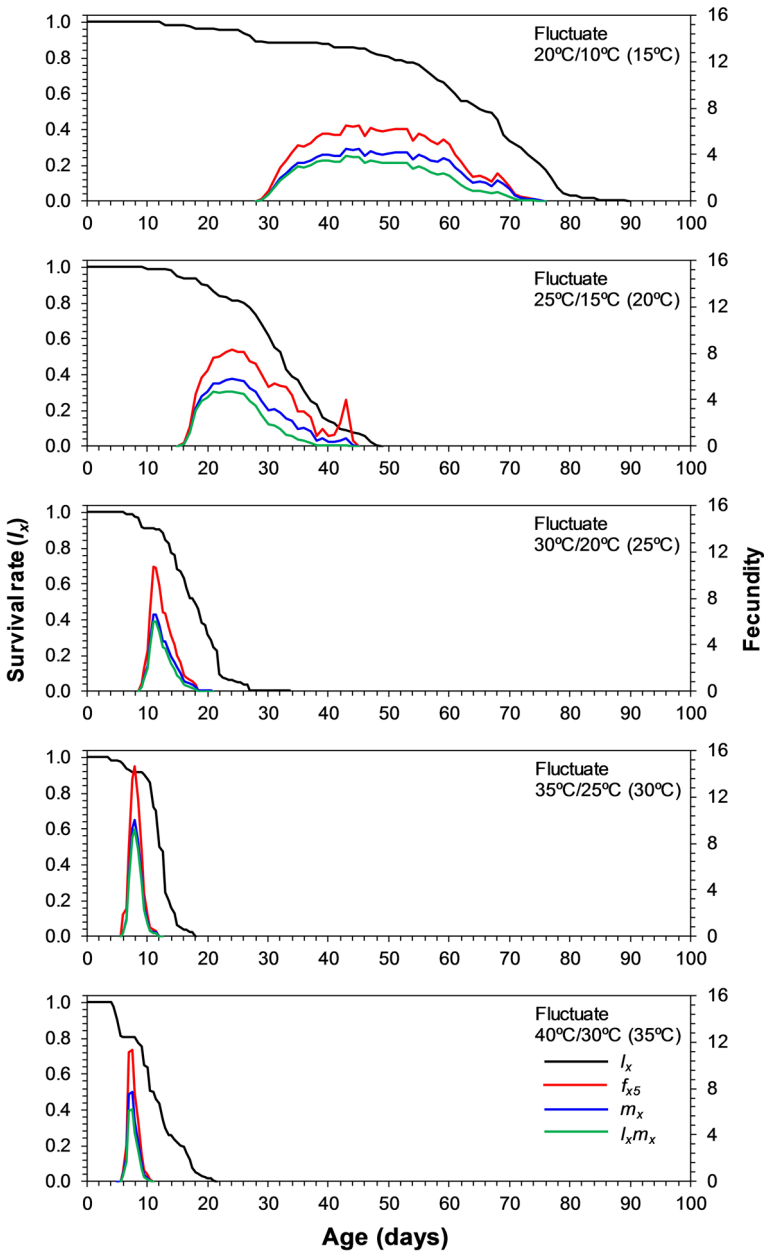


Fig. 5 Age-specific survival rate (l_x), fecundity (m_x), maternity ($l_x m_x$) and age-stage-specific fecundity ($f_{x,5}$) of *Tetranychus urticae* at five fluctuating temperatures

higher at fluctuating temperatures in the lower temperature range, whereas lower development rates were observed at higher fluctuating temperatures compared with the corresponding constant temperature regimes. Furthermore, lower thermal thresholds were higher at constant compared to fluctuating temperatures. This finding indicates that spider

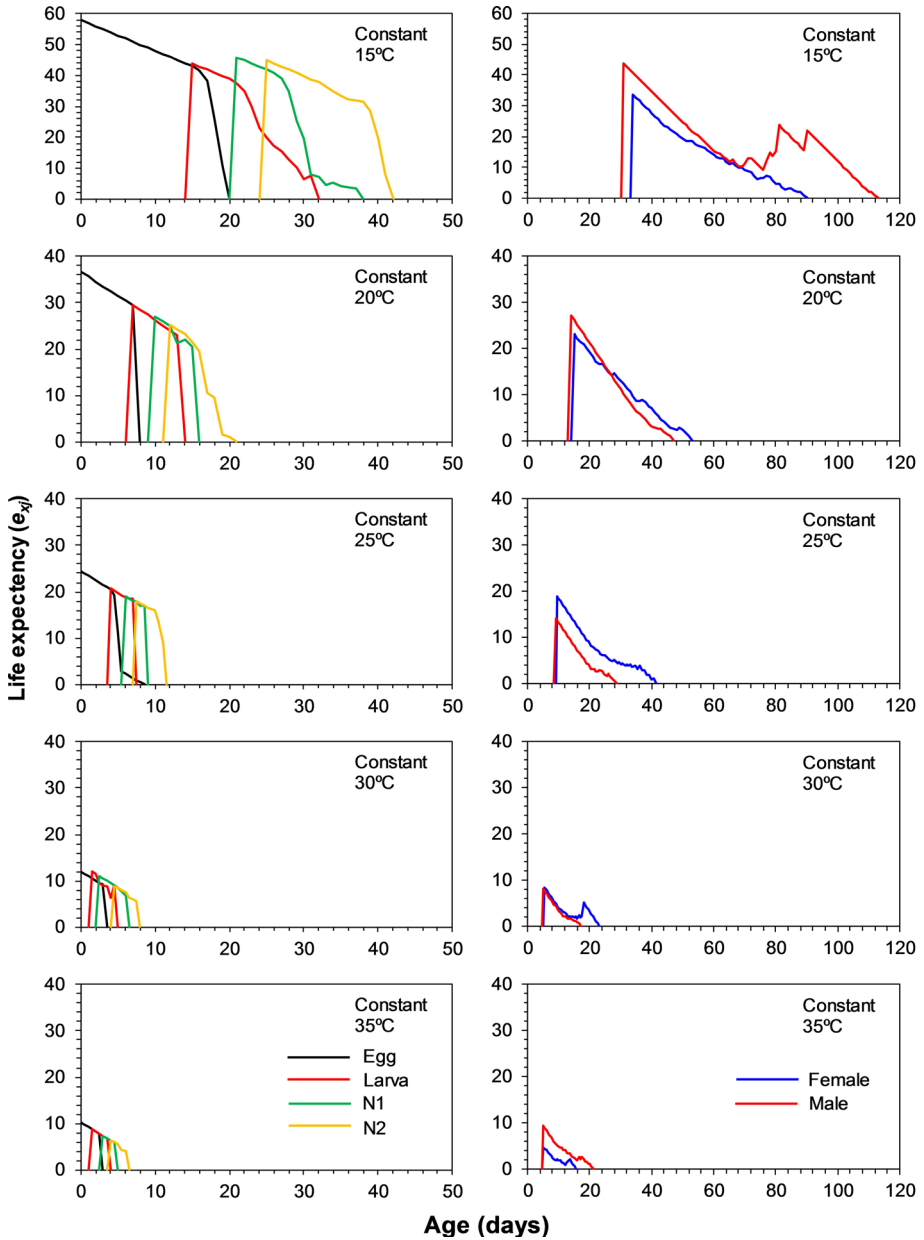


Fig. 6 Age-stage-specific life expectancies (e_{xj}) of *Tetranychus urticae* at five constant temperatures. *Left panels* depict different life stages and *right panels* depict different adult sexes

mites can adapt and develop at temperatures lower than the lower thermal threshold if the warm-phase temperatures exceed the threshold temperatures under fluctuation conditions.

In the present study, the immature survival rates were significantly higher under fluctuating temperatures compared with those under the corresponding constant temperatures

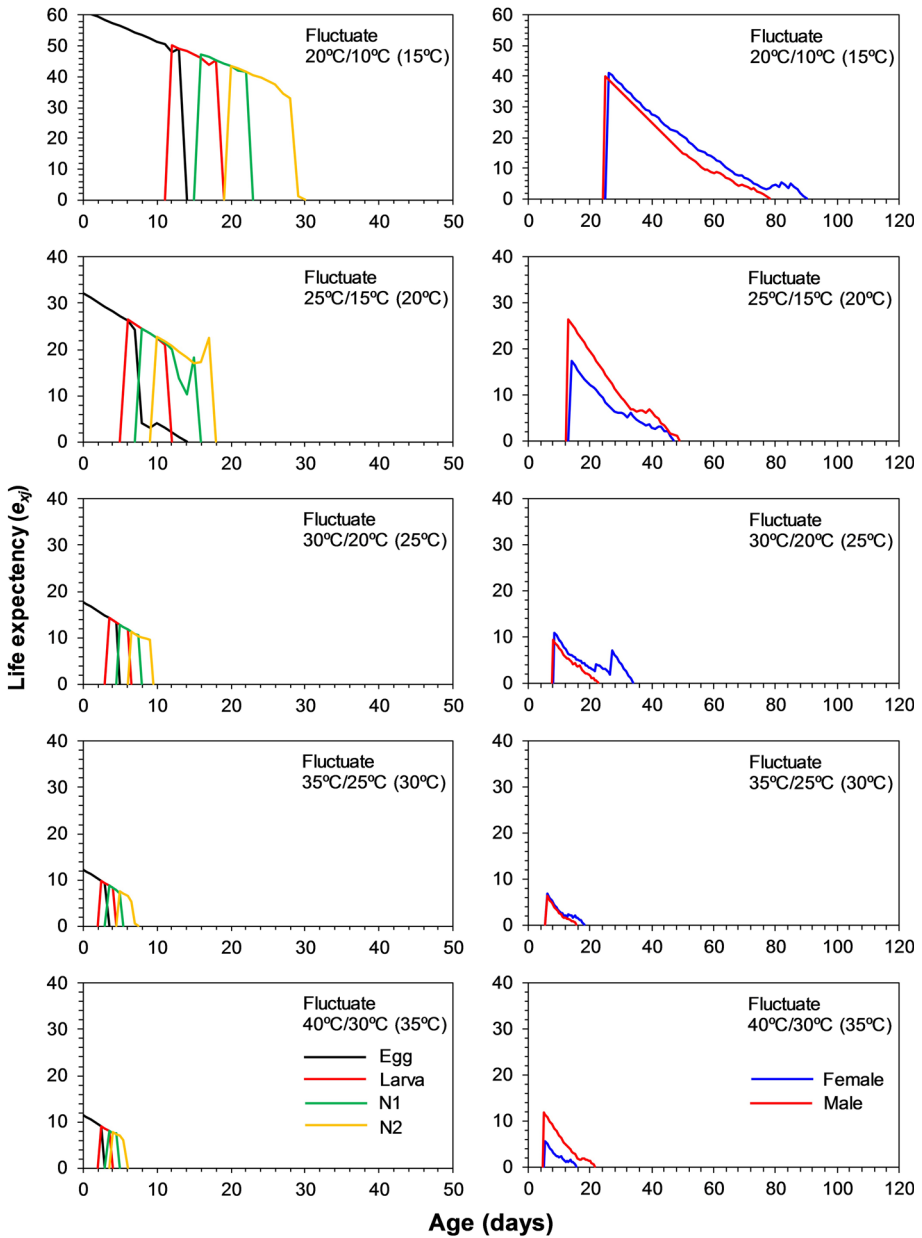


Fig. 7 Age-stage-specific life expectancies (e_{xj}) of *Tetranychus urticae* at five fluctuating temperatures. *Left panels* depict different life stages and *right panels* depict different adult sexes

of 17.5 °C and below, and did not significantly differ at 20 °C and higher. A possible explanation is that the exposure to low temperatures disrupts ion homeostasis (MacMillan et al. 2012). Under fluctuating temperatures, the injuries caused during the cool phase are repaired during the warm phase by reestablishing the ionic balance (Collinet et al. 2007;

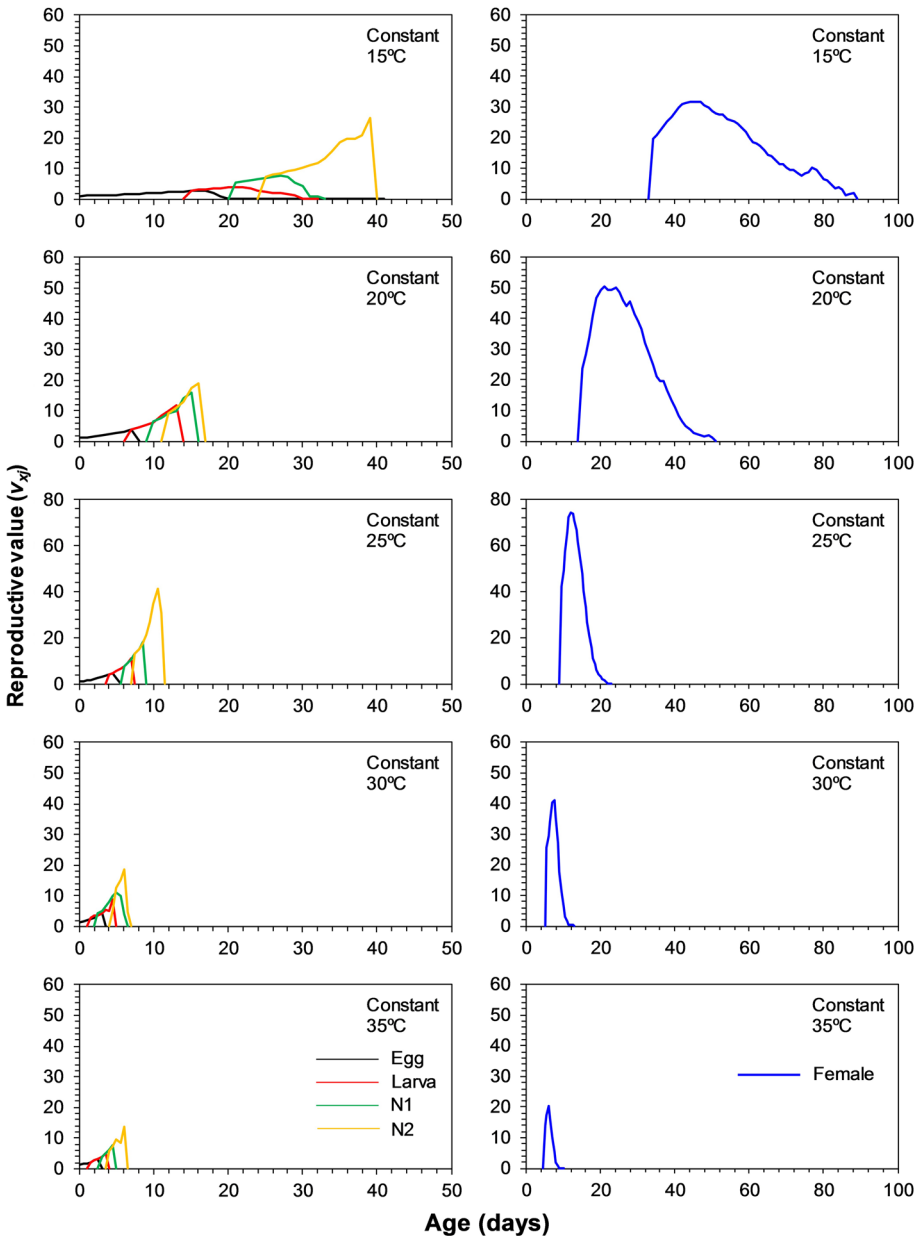


Fig. 8 Age-stage-specific reproductive values (v_{xj}) of *Tetranychus urticae* at five constant temperatures. *Left panels* depict different life stages and *right panels* depict female adult

MacMillan et al. 2012). The reduced development times under fluctuating temperature regimes at lower temperatures may interfere with gene transcription, protein translation and increasing the number of divergent proteins (Collinet et al. 2007; Delava et al. 2016). The warm phase would allow up-regulation of heat-shock protein (*Hsp*), and this process

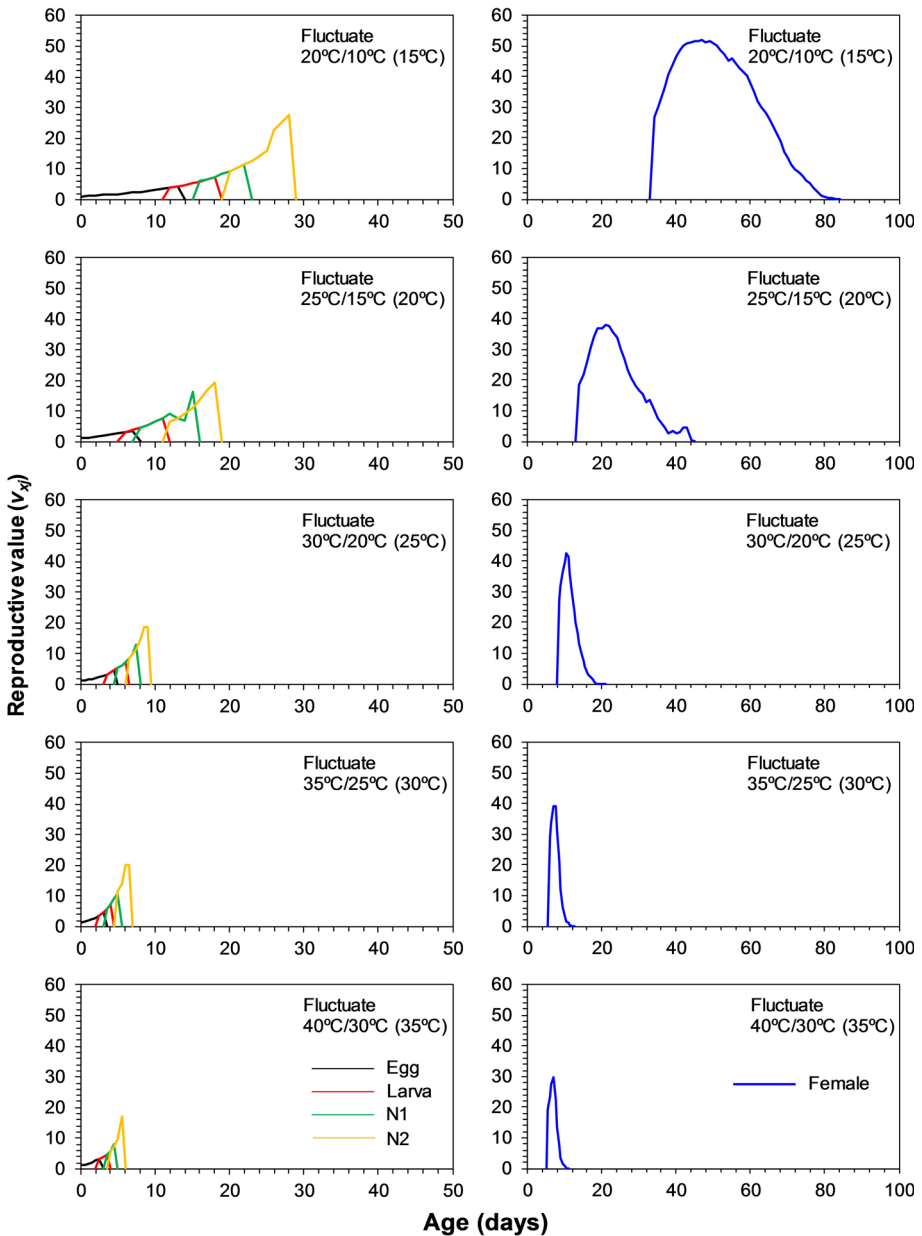


Fig. 9 Age-stage-specific reproductive values (v_{xj}) of *Tetranychus urticae* at five fluctuating temperatures. *Left panels* depict different life stages and *right panels* depict female adults

would prevent the disaggregation of denatured proteins (Collinet et al. 2007). Fluctuating temperatures are more favorable compared with constant temperatures, especially in extreme conditions, by reducing the effect of stressful temperatures and inducing physiological stress that impacts the insect survivorship (Marshall and Sinclair 2010).

Table 3 Demographic parameters (R_0 , net reproductive rate; r , intrinsic rate of increase; λ , finite rate of increase; T , mean generation time) of *Tetranychus urticae* on bean leaf discs at constant and fluctuating temperatures under a 24:0 h L: D photoperiod

Temperature (°C)	Net reproductive rate (R_0)	Intrinsic rate of natural increase (r)	Finite rate of increase (λ)	Mean generation time (T)
Constant				
15	30.78 ± 3.82Bh	0.063 ± 0.002Bi	1.065 ± 0.0022Bi	54.12 ± 0.61Aa
20	88.28 ± 8.11Ac	0.170 ± 0.003Ag	1.185 ± 0.0039Ag	26.42 ± 0.21Ac
25	93.04 ± 8.37Ab	0.314 ± 0.006Ae	1.369 ± 0.0088Ae	14.42 ± 0.09Ae
30	38.58 ± 3.76Ag	0.423 ± 0.011Ab	1.526 ± 0.0171Ab	8.64 ± 0.06Ag
35	16.87 ± 1.69Bj	0.400 ± 0.013Ac	1.491 ± 0.0198Ac	7.07 ± 0.06Bj
Fluctuating ^a				
20/10 (15)	99.79 ± 7.96Aa	0.104 ± 0.002Ah	1.109 ± 0.0020Ah	44.32 ± 0.30Bb
25/15 (20)	59.08 ± 5.70Bd	0.170 ± 0.004Ag	1.185 ± 0.0044Ag	24.04 ± 0.19Bd
30/20 (25)	43.34 ± 4.47Be	0.303 ± 0.008Af	1.355 ± 0.0101Af	12.42 ± 0.11Bf
35/25 (30)	40.62 ± 3.28Af	0.438 ± 0.009Aa	1.550 ± 0.0145Aa	8.45 ± 0.06Bh
40/30 (35)	23.02 ± 2.58Ai	0.392 ± 0.013Ad	1.480 ± 0.0195Ad	8.00 ± 0.05Ai

^a Mean temperature in parentheses

Different upper case letters following means within a column denote significant differences between constant and fluctuating condition at the same (mean) temperature, whereas different lower case letters following means denote significant differences among temperatures based on the paired bootstrap test ($P < 0.05$)

Previous researchers found that the development time of arthropods decreased with increasing temperature (Fantinou et al. 2003; Ullah et al. 2011, 2012; Vangansbeke et al. 2013, 2015; Gotoh et al. 2010, 2014; Mironidis 2014; Ullah and Lim 2015). Our results are consistent with those previous studies, because development time decreased as temperature increased under both constant and fluctuating temperatures. This phenomenon occurs because of the acceleration of biochemical processes at higher temperatures (Atkinson 1996). Compared with the corresponding constant temperatures, the *T. urticae* development rate tends to be higher at lower fluctuating temperature ranges, lower at higher fluctuating temperature ranges, and minimally different at intermediate temperature ranges, which is consistent with the results of Vangansbeke et al. (2013). Additionally, we cannot ignore indirect effects of the diurnal temperature range on *T. urticae* development via leaf disc nutritional value. For example, temperature variations have been reported to alter the levels of gibberellin in different plant species (Myster and Moe 1995; Stavang et al. 2005), which may affect the performance of *T. urticae* that feed on those plants (Eichmeier and Guyer 1960). It is possible that the levels of other components are also affected by diurnal temperature range, which subsequently influences herbivore performance.

Fluctuating temperatures had a significant effect on all reproductive parameters, but the effect differed among the tested temperatures. Fluctuating temperatures with a mean of 15 °C led to significantly higher fecundity compared with the corresponding constant temperature of 15 °C. Some studies that investigated the fecundity of insects under constant and fluctuating temperatures found that more eggs were produced under fluctuating conditions (Davis et al. 2006; Vangansbeke et al. 2013), but some studies also reported no effect of fluctuating temperatures on insect fecundity (Hagstrum and Leach 1973; Ullah

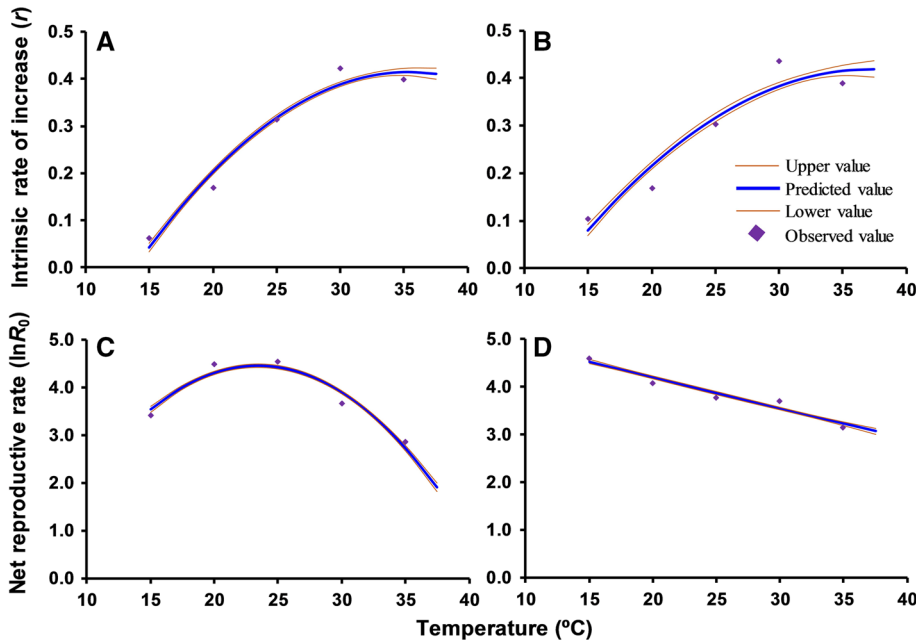


Fig. 10 Effect of temperature and/or conditions on intrinsic rate of increase (r) and net reproductive rate (R_0) of *Tetranychus urticae*. Variation of r under constant (a) and fluctuating (b) conditions, and of $\ln(R_0)$ under constant (c) and fluctuating (d) conditions. The thick lines (blue) for r and R_0 show the predictions, based on the generalized linear models after eliminating non-significant terms. Thin lines (brown) show the 95% confidence limits for the predictions. The diamond shapes indicate the observed values

and Lim 2015). Temperature fluctuation may facilitate better adaptations or recovery periods that result in higher fecundity under extreme high or low temperature conditions (Davis et al. 2006). Lifetime and daily fecundity of *T. urticae* under fluctuating temperatures in our study were higher than the values of Vangansbeke et al. (2013), even though both studies had the same mean temperature of 15 °C (20/5 °C; 16 h at 20 °C and 8 h at 5 °C). The possible reasons for variation between the two studies include differences in geographical populations, temperature amplitude and photoperiod, which may impact the changes in reproductive parameters. A high level of temperature fluctuation dramatically changes the climatic stress resistance for certain physiological response of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Terblanche et al. 2010; Foray et al. 2014). The temperature amplitudes affected *T. urticae* development and reproduction, and as a result the oviposition period, lifetime fecundity and adult longevity gradually decreased with increasing amplitude (Gotoh et al. 2014).

Geographical variation is known to have a significant impact on life history parameters. A higher elevation region (1314 m above sea level) with a lower mean temperature (16.3 °C) induced higher fecundity and population parameters in the beet armyworm, *Spodoptera exigua* (Hübner), compared with those collected from a lower elevation region (31.9 m above sea level) and higher mean temperature (19 °C) (Golikhajeh et al. 2016). Another reason might be photoperiod, which could explain the differences in *T. urticae* development time found by Vangansbeke et al. (2013) despite their use of the same mean temperature of 15 °C. Our study was conducted under a 24L:0D photoperiod, but the Vangansbeke et al. (2013) study was conducted under a 16L:8D photoperiod. Photoperiod

is known to affect growth rate, development time and other physiological aspects of arthropods (Lopatina et al. 2011; Wang et al. 2013; Zerbino et al. 2013; Zou et al. 2016). However, the photoperiodic effect is not straightforward: a certain photophase can slow the development rate of insects compared with another photophase at one temperature, whereas it may accelerate development at another temperature (Lopatina et al. 2011). Photoperiod also influences insect longevity and reproduction (Malaquias et al. 2010; Wang et al. 2013; Zerbino et al. 2013; Zou et al. 2016). Longer longevity and higher fecundity were observed in the spined soldier bug, *Podisus nigrispinus* (Dallas), when reared under a longer photoperiod compared with shorter photoperiod (Malaquias et al. 2010). However, a long photophase might increase nutritional intake, which could have a positive impact on fecundity.

Life history parameters are important to help forecast and hence improve control strategies for the economically important *T. urticae*. The intrinsic rate of increase reflects combined effects of several biological parameters, including the first reproductive stage, fecundity, peak of reproduction, length of the reproductive period and survival rate. Previous studies demonstrated that the impact of fluctuating temperatures on insects and mites differed among species: fluctuating temperatures can enhance the population growth rate of some insects and mites, such as *Helicoverpa armigera* (Hübner) (Mironidis and Savopoulou-Soultani 2008), *T. urticae* (Vangansbeke et al. 2013; Gotoh et al. 2014), *Frankliniella occidentalis* (Pergande) and *Frankliniella intonsa* (Trybom) (Ullah and Lim 2015). The r value at fluctuating temperatures with a mean of 15 °C can enhance the population growth rate compared with the corresponding constant temperature, which is different from Vangansbeke et al.'s (2013) findings. This variation might be owing to use of different strains and computation of life table parameters using a traditional female age-specific life table, which ignores some important factors, such as male individuals and stage differentiation. Both males and females are economically important and affect population dynamics (Huang and Chi 2012; Sugawara et al. 2017).

Our results indicate that fluctuating temperatures influence *T. urticae* development rates, impact on their reproductive capacities and affect their population growth, which are differed from those under constant temperatures. Hence, fluctuating temperatures need to be considered to predict population dynamics in nature.

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