Temperature-dependent development and reproductive traits of *Tetranychus macfarlanei* (Acari: Tetranychidae)

Mohammad Shaef Ullah · Md. Ahsanul Haque · Gösta Nachman · Tetsuo Gotoh

Abstract Development and reproductive traits of *Tetranychus macfarlanei* Baker & Pritchard (Acari: Tetranychidae) were investigated on kidney bean, *Phaseolus vulgaris* L., at eleven constant temperatures. *Tetranychus macfarlanei* was able to develop and complete its life cycle at temperatures ranging from 17.5 to 37.5°C. At 15 and 40°C, a few eggs (2–4%) hatched but further development was arrested. Development from egg to adult was

In a recent paper, Ali et al. (2011; insectscience.org/11.167) reported that *Tetranychus macfarlanei* occurs in Bangladesh, India, Madagascar, Mauritius, Thailand, Japan, Taiwan, USA, Malaysia, and the Canary Islands, based on 'personal communication'. However, to date this species is reported only from India, Madagascar, Mauritius and the Canary Islands, and in the current paper we newly add Bangladesh. *Tetranychus macfarlanei* is not known from Japan and its geographical distribution is fabricated in the paper by Ali et al. Mr. Ali confessed to TG that voucher specimens of *T. macfarlanei* were not deposited, simply because the authors did not collect the species in Japan or any of the other countries mentioned.

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slowest at 17.5°C and fastest at 35°C for both females and males. Using Ikemoto and Takai's linear model, the estimated lower developmental thresholds for egg-to-female adult, egg-to-male adult and egg-to-egg development were 12.9–13.0°C. The thermal constants for the respective stages were 110.85, 115.99 and 125.32 degree-days (DD). The intrinsic optimum temperatures (T_Φ) calculated by non-linear SSI model were determined as 24.4, 24.4 and 24.2°C for egg-to-female adult, egg-to-male adult and egg-to-egg development, respectively. The net reproductive rate (R_0) was highest at 25°C (167.4 females per female) and lowest at 17.5°C (42.6 females per female). The intrinsic rate of natural increase, r_m, increased linearly with the rising of temperature from 0.102 at 17.5°C to 0.441 day^{-1} at 35°C. These values suggested that *T. macfarlanei* could be growing quickly in response to increasing temperatures from 17.5 to 35°C and provide a basis for predicting its potential geographical range.

Keywords *Tetranychus macfarlanei* · Development · Demographic parameter · Degree-day · Intrinsic rate of natural increase

Introduction

Life processes are closely associated with environmental factors and of them temperature is the dominant abiotic factor for development and reproduction in poikilothermic arthropods; i.e., temperature affects essential population processes such as development rate, birth rate, death rate, fecundity and generation time, and as a result drives population growth traits of target species (Campbell et al. 1974; Roy et al. 2002; Gotoh et al. 2010; Ullah et al. 2011). Knowing the temperature requirements of the various life stages of a target species is instrumental in forecasts of its potential distribution and population dynamics. The ability of a pest to develop at different temperatures determines to a large extent of its survival under different climatic conditions (tropical, subtropical and temperate regions), which is important in predicting pest outbreaks. The intrinsic rate of natural increase (r_m) is a common indicator to describe and evaluate the growth and adaptation of a population of arthropods to certain environmental conditions (Birch 1948). The r_m-value can be determined from the life history components of organisms, such as developmental rate, ovipositional rate, survival rate and the proportion of females in the offspring (Sabelis 1985). The r_m-value is a key demographic parameter used for predicting the potential severity of a pest species (Margolies and Wrensch 1996; Gotoh et al. 2004, 2010). Differences in r_m-values among temperatures affect how rapid poikilothermic arthropods such as insects and mites can increase on their host plants. The validity of this general life history prediction can be tested by a comparison of r_m-value, degree of polyphagy and pest status (Sabelis 1985, 1991; Gotoh et al. 2003).

The spider mite *Tetranychus macfarlanei* Baker & Pritchard has been reported from India, Madagascar, Mauritius and the Canary Islands, and can infest a wide range of crops in the families Malvaceae, Fabaceae, Cucurbitaceae, Convolvulaceae and Solanaceae (Jeppson et al. 1975; Bolland et al. 1998). Symptoms of infestation by *T. macfarlanei* first appear on leaves, as a pronounced yellowish hue, then the leaves wilt and finally drop, especially during dry periods (Moutia 1958). *Tetranychus macfarlanei* is new to Bangladesh, but it has spread throughout the country and causes serious damage to a variety of crops such as jute, bean, eggplant and bottle gourd (Haque et al. unpublished data). There are no published studies on the effects of temperature on development and reproduction of *T. macfarlanei*. Given this lack of information on the ecology of *T. macfarlanei*, we

initiated a study of the effect of temperature on development and reproduction of *T. macfarlanei*, and disclosed its basic thermal requirements for development. Our purpose was to develop a comprehensive understanding of the effects of temperature on the population dynamics of *T. macfarlanei*.

Materials and methods

Spider mite

Tetranychus macfarlanei was initially collected on 27 August 2009 from a bean field (*Lablab purpureus* (L.) Sweet) at the Bangladesh Agricultural Research Institute, Bangladesh (24°00′N, 90°24′E). The *T. macfarlanei* strain was imported to Japan with the authorization of the Ministry of Agriculture, Forestry and Fisheries of Japan (No. 21Y421). All experiments with *T. macfarlanei* were conducted in a level P_2 biohazard room under negative pressure hood and the residual individuals as well as trash were autoclaved before discarding. Laboratory stocks were maintained on leaf discs (ca. 16 cm^2) of kidney bean, *Phaseolus vulgaris* L., placed on water-saturated polyurethane mats in plastic dishes (90 mm diameter, 20 mm depth) at 25 ± 1°C, 60–70% RH, and a photoperiod of 16: 8 h light: dark.

Immature development

Inseminated adult females obtained from stock cultures were transferred individually onto a leaf disc (2 × 2 cm) of kidney bean and kept at one of eleven constant temperatures, ranging from 15 to 40°C at a 2.5°C interval, under a long day photoperiod (16L: 8D) with 60–70% RH. Females were allowed to lay eggs for 24 h at 15–25°C, for 12 h at 27.5–35°C or for 6 h at 37.5–40°C. Only one egg was left and reared on the leaf disc, and the developmental stages were recorded at the same time every day until all individuals reached the adult stage. Some eggs did not hatch and some immatures drowned—they were included in the calculation of the survival rate, but did not include them in the calculation of developmental duration.

Reproduction and female longevity

When a female teleiochrysalis appeared in the developmental experiments, two adult males obtained from stock cultures were introduced onto the leaf disc for mating and then removed 24 h after emergence of the adult female. To determine the pre-oviposition period at the respective temperatures, we observed the leaf discs at 6- to 24-h intervals (depending on temperature—the shortest intervals were applied at the highest temperatures). Newly emerged females obtained from the above-mentioned experiments at 17.5, 20, 25, 30 and 35°C, were used to assess their reproductive traits and longevity. The number of eggs laid by a female was recorded daily throughout her life to determine oviposition period, total number of eggs laid per female, eggs laid per female per day, post-oviposition period and female longevity. Eggs laid were removed daily by means of tweezers. During the oviposition period, some adult females drowned, especially just after replacing the leaf discs, or were killed accidentally. These females were discarded from the analysis. Adult mites were transferred onto new leaf discs using a fine brush at 1- to 2-week intervals.

Hatchability, survivability and sex ratio

To calculate age-specific survival rate (l_x) and age-specific fecundity rate (m_x), we assessed egg hatchability, the survival rate of immature stages and the proportion of female offspring at 17.5, 20, 25, 30 and 35°C. To obtain these data, a single teleiochrysalis female and two adult males, which were maintained from eggs at the respective temperatures, were placed on a leaf disc (ca. 16 cm^2) of kidney bean for copulation, and the females were allowed to lay eggs for five days after the pre-oviposition period. The eggs obtained from each female were maintained to determine the above-mentioned parameters after reaching adulthood.

Life-table parameters

Life table and fertility tables were calculated using the data obtained from the various experiments. The intrinsic rate of natural increase (r_m) was estimated from the fecundity table according to the equation given by Birch (1948): $\sum e^{-r_m x} l_x m_x = 1$, where x is female age in days, l_x is the age-specific survival rate [(proportion of females surviving at age x) × (rate of egg hatchability) × (survival rate of immature stages)] and m_x is the expected number of daughters produced per female alive at age x [(age-specific oviposition) × (proportion of females)] (Sabelis 1985; Gotoh and Gomi 2003; Gotoh et al. 2010; Ullah et al. 2011). The net reproductive rate (R_0) is given by $R_0 = \sum l_x m_x$, the mean generation time (t_G) in days is given by $t_G = \ln R_0 / r_m$, the finite rate of increase (λ) is given by $\lambda = e^{r_m}$, and the doubling time (t_D) in days is $t_D = \ln 2 / r_m$. After r_m was computed from the original data (r_{all}), the standard errors for the life-table parameters at different constant temperatures were estimated using the Jackknife method (Meyer et al. 1986; Maia et al. 2000). Briefly, one of the mites is omitted and r_m (r_i) is calculated for the remaining mites ($n - 1$). Based on Meyer et al. (1986), the Jackknife pseudo-value (r_j) is computed for this subset of the original data according to the equation $r_j = n \, r_{all} - (n - 1) \, r_i$. This process was repeated for all possible omissions of one mite from the original data set to produce pseudo-values which allowed for computing confidence limits for the parameter values.

Effect of temperature on mite developmental rate

The reciprocal of developmental time in days is denoted as developmental rate. These rates are used in linear and non-linear models. The thermal constant and lower threshold temperature were determined using the line-fitting method proposed by Ikemoto and Takai (2000). The data points that deviated from the straight line were not used to fit the linear model. The law of total effective temperature applied to the temperature-dependent development of arthropods is expressed by the equation:

$$D = \frac{k}{T - t} \quad [\text{for } T > t],$$

where D is the duration of development (days), T is environmental (mean/isothermal) temperature (°C), t the lower threshold temperature, and k the thermal constant. The developmental rate, defined as the reciprocal of D, increases linearly with T according to:

$$\frac{1}{D} = -\frac{t}{k} + \frac{1}{k} T \quad [\text{for } T \geq t].$$

The linear Ikemoto and Takai approximation enables to calculate two constants: the lower developmental threshold and the thermal constant or the sum of total effective

temperature, within a limited temperature range. On the other hand, the non-linear thermodynamics model describes the developmental rate over a wide range of temperatures and estimates of optimum temperatures for development. The equation of the non-linear thermodynamics (Sharpe-Schoolfield-Ikemoto [SSI]) model can be expressed as follows (Ikemoto 2005, 2008; Shi et al. 2011):

$$r([T]) = \frac{\rho \frac{[T]}{[T_\Phi]} \exp\left[\frac{\Delta H_A}{R}\left(\frac{1}{[T_\Phi]} - \frac{1}{[T]}\right)\right]}{1 + \exp\left[\frac{\Delta H_L}{R}\left(\frac{1}{[T_L]} - \frac{1}{[T]}\right)\right] + \exp\left[\frac{\Delta H_H}{R}\left(\frac{1}{[T_H]} - \frac{1}{[T]}\right)\right]},$$

where r represents the developmental rates (the dependent variables) at the absolute temperature ($[T]$) (the independent variable). All the other parameters are constants: $[T_L]$, $[T_H]$, and $[T_\Phi]$ represent absolute temperatures—$[T_L]$ and $[T_H]$ represent temperatures below (L) and above (H) an optimum temperature, at which an enzyme is 50% active –, ΔH_A, ΔH_L, and ΔH_H represent enthalpy changes, R is the universal gas constant, and ρ is the development rate at $[T_\Phi]$. $[T_\Phi]$ is the intrinsic optimum temperature for development that exhibits the minimum effects on enzyme inactivation related to development at low and high temperature (Ikemoto 2005) and it is expressed as follows:

$$[T_\Phi] = \frac{\Delta H_L - \Delta H_H}{R \ln\left(-\frac{\Delta H_L}{\Delta H_H}\right) + \left(\frac{\Delta H_L}{[T_L]}\right) - \left(\frac{\Delta H_H}{[T_H]}\right)}.$$

Statistical analysis

Data were analyzed by means of analyses of covariance (ANCOVA), using temperature as the covariate. The purpose was to quantify relationships between the response variables (eggs/female, hatchability, survival rate, female ratio, oviposition period, female longevity, egg-to-adult developmental time, total oviposition, net reproductive rate, and intrinsic rate of natural increase, generation time and lambda) and predictor variables for egg-to-adult developmental time (gender and temperature) in order to identify which of the predictor variables contributes most to explain the variation in data. All models included a third-order term of temperature, but only significant terms were included in the final model. The full ANCOVA model for analyzing all response variables reads:

$$y = \beta_0 + \beta_1 G + \beta_2 T + \beta_3 T^2 + \beta_4 GT + \beta_5 GT^2 + \varepsilon,$$

where y is the response variable, β_i is the parameter associated with the i-th term, G gender, T temperature, and ε the residual error. All response variables were analyzed by means of Generalized Linear Models (McCullagh and Nelder 1989) using PROC GENMOD (Enterprise Guide 4.1, SAS Institute 2006). The advantage of GENMOD is that it permits data with non-normal distributions. Proportions (female ratio, hatchability and survival rate) are likely to be binomially distributed, discrete numbers (eggs/female) to be Poisson or negative binomially distributed, whereas the continuous variables (developmental duration, oviposition period, adult longevity, R_0, r_m, t_G and λ) are likely to be normally distributed. When needed, continuous variables were subjected to a logarithmic (ln) transformation in order to stabilize the variance and to ensure that the back-transformed values were non-negative.

To test for differences in temperature responses between genders, we compared the deviance of the full model with the increase in deviance resulting from omitting genders from the full model. The difference was tested by means of Manly's (1990) test:

$$Fv_1, v_2 = \frac{(D_1 - D_2)/(p_2 - p_1)}{D_2/(N - p_2 - 1)}$$

where D_1 and D_2 denote the deviance of the reduced and the full model, respectively, p_1 and p_2 are the number of parameters of the reduced and full model, and N is the total number of observations in the data set. The degrees of freedom were calculated as $v_1 = p_2 - p_1$ and $v_2 = N - p_2 - 1$. Likewise, the effects of temperature and gender were assessed by comparing deviances of models with and without temperature and gender, respectively.

Results

Immature development

At temperatures ranging from 17.5 to 37.5°C, both the female and male of *T. macfarlanei* completed their development from egg to adult. Very few eggs of *T. macfarlanei* hatched at 15°C (2/96 eggs) and 40°C (4/96 eggs), but they died at the larval stage. These data were not used in any subsequent analysis. Developmental time from egg to adult was significantly affected by temperature (Tables 1, 2; Appendix 1). The developmental time from egg to adult was decreased with increasing temperatures until 35°C and then increased at 37.5°C (Fig. 1; Appendix 1). The developmental time differed significantly between females and males ($F_{3,795} = 31.468$, $p < 0.001$).

Ikemoto and Takai's linear method, fitting the development rate values, gave a close fit for the 17.5–35°C range of temperatures ($0.993 \le r^2 \le 0.996$) (Table 3; Fig. 2; Appendix 1). The estimated lower threshold temperatures ($T_L = t$) for egg-to-female adult, egg-to-male adult and egg-to-egg development were very similar: 12.9–13°C (Table 3). The thermal constants (k) for the respective stages of *T. macfarlanei* were 116.0, 110.9 and 125.3 degree-days (DD) (Table 3). The non-linear SSI model fitted the development rates closely in the temperature range between 17.5 and 37.5°C ($0.0021 \le \chi^2 \le 0.0024$) (Table 3; Fig. 2). The intrinsic optimum temperature (T_Φ) for egg-to-female adult, egg-to-male adult and egg-to-egg development was 24.2–24.4°C (Table 3).

Reproduction

The pre-oviposition period decreased with increasing temperatures from 17.5 to 35°C (Table 4; Appendix 1). The oviposition period, post-oviposition period, adult longevity and daily egg production (eggs/female/day) were strongly affected by temperature (Tables 1, 2; Fig. 3). The oviposition period was lowest at 35°C. Adult longevity decreased with increasing temperatures from 17.5 to 35°C. Fecundity (eggs/female) was highest at 25 and 30°C (Fig. 3).

The effects of temperature on the number of eggs laid during the first five days of the oviposition period, their hatchability, the survival rate of immature stages and the proportion of female offspring were highly significant ($p < 0.001$; Table 1, Fig. 4; Appendix 3). Number of eggs laid during the first five days of the oviposition period increased with increasing temperatures from 17.5 to 30°C and then slightly decreased at 35°C. Hatchability and survival rate of immature stages increased with increasing temperatures and peaked at around 20–30°C followed by a small decline at 35°C. Offspring female ratio peaked at around 20–35°C. The models describing temperature responses are given in Table 2.

Table 1 Results of the statistical analyses based on PROC GENMOD for analyzing all response variables of *Tetranychus macfarlanei*

Response variable	Distribution	Deviance[a]	
		Null model	Full model[b]
Egg-to-adult development[c]	Normal[d]	187.24	4.66 ($F_{5,795} = 6234.01$***)
Eggs/female after 5 days oviposition	Negative binomial[d]	110319.11	184.08 ($F_{2,190} = 56839.19$***)
Hatch rate after 5 days oviposition	Binomial[e]	390.13	286.92 ($F_{2,190} = 34.17$***)
Juv. survival rate after 5 days oviposition	Binomial[e]	379.73	275.28 ($F_{2,190} = 36.05$***)
Sex ratio after 5 days oviposition	Binomial[e]	89.40	79.27 ($F_{2,190} = 12.14$***)
Oviposition period	Normal[d]	41.11	19.68 ($F_{2,201} = 109.44$***)
Female longevity	Normal[f]	50.51	20.59 ($F_{2,201} = 146.04$***)
Total oviposition/female	Negative binomial[d]	976397.18	210.80 ($F_{2,201} = 465401.95$***)
Net reproduction rate (R_0)	Normal[f]	59.52	0.96 ($F_{2,201} = 6130.50$***)
Intrinsic rate of increase (r_m)	Normal	3.43	0.09 ($F_{2,201} = 3729.67$***)
Mean generation time (t_G)	Normal[f]	48.12	1.35 ($F_{2,201} = 3481.77$***)
Finite rate of increase (λ)	Normal	6.01	0.20 ($F_{2,201} = 2919.53$***)

*** $p < 0.001$

[a] Deviance is a measure of model quality. The lower the deviance relative to the deviance of the null model is, the better the fit

[b] Full model also includes gender and its interaction with temperature

[c] Full model includes gender, temperature and temperature². The F test measures whether the full model is significantly better than the null model

[d] The link fuction used in PROC GENMOD is the logarithmic function

[e] The link fuction used in PROC GENMOD is the logit function

[f] Dependent variable was subjected to a logarithmic transformation prior to analysis

Life-table parameters

The age-specific survival rate (l_x) started to drop at earlier ages as the temperature increased from 17.5 to 35°C (Fig. 5). The age-specific fecundity rate (m_x) peaked at earlier ages and the width of the peak, i.e. the oviposition period, was apt to become narrower as the temperature raised from 17.5 to 35°C. The first egg laying was recorded on days 28, 16, 12, 8 and 6 at 17.5, 20, 25, 30 and 35°C, respectively. Daily egg production reached a peak of 4.6 eggs on day 36 at 17.5°C, 9.4 eggs on day 23 at 20°C, 12.5 eggs on day 18 at 25°C, 16.6 eggs on day 13 at 30°C, and 14.1 eggs on day 9 at 35°C. Female adults started to die on days 43, 27, 24, 16 and 10 at the respective temperatures. At 17.5, 20, 25, 30 and 35°C, all females had died on days 72, 59, 46, 30 and 23 at the respective temperatures.

The net reproductive rate (R_0), the intrinsic rate of natural increase (r_m), the mean generation time (t_G), and the finite rate of increase (λ) were significantly affected by temperature (Tables 1, 2; Fig. 6). The highest R_0-value was observed at 25°C, whereas the lowest value was found at 17.5°C (167.4 vs. 42.6) (Appendix 4). The r_m and λ values increased with increasing temperatures from 17.5 to 35°C. The highest r_m-value was observed as 0.441 day^{-1} at 35°C and the lowest value was observed as 0.102 day^{-1} at

Table 2 Temperature response of *Tetranychus macfarlanei*

Response variable	n	Linear predictor[a]
Egg-to-adult development (female)[b]	497	$y = 7.0352(0.0704) - 0.2896(0.0053)T + 0.0039(0.0001)T^2$
Egg-to-adult development (male)[b]	304	$y = 6.9686(0.0912) - 0.2909(0.0067)T + 0.0040(0.0001)T^2$
Eggs/female after 5 days oviposition[b]	193	$y = -4.7081(0.3027) + 0.5627(0.0229)T - 0.0088(0.0004)T^2$
Hatch rate after 5 days oviposition[c]	193	$y = -4.3101(1.7199) + 0.6489(0.1285)T - 0.0131(0.0023)T^2$
Juv. survival after 5 days oviposition[c]	193	$y = -3.0574(1.9378) + 0.5812(0.1432)T - 0.0121(0.0026)T^2$
Sex ratio after 5 days oviposition[c]	193	$y = 0.2267(0.5281) + 0.1008(0.0400)T - 0.0015(0.0007)T^2$
Oviposition period[b]	204	$y = -0.3120(0.4491) + 0.2954(0.0364)T - 0.0065(0.0007)T^2$
Female longevity[b]	204	$y = 1.5626(0.4593) + 0.1746(0.0372)T - 0.0045(0.0007)T^2$
Total oviposition/female[b]	204	$y = -5.1362(0.4491) + 0.7831(0.0362)T - 0.0146(0.0007)T^2$
Net reproductive rate (R_0)[b]	204	$y = -6.3261(0.0991) + 0.8600(0.0080)T - 0.0160(0.0002)T^2$
Intrinsic rate of increase (r_m)	204	$y = 0.2250(0.1769) - 0.0508(0.0214)T + 0.0034(0.0008)T^2 - 0.0001(0.0000)T^3$
Mean generation time (t_G)[b]	204	$y = 5.9365(0.1175) - 0.1665(0.0095)T + 0.0017(0.0002)T^2$
Finite rate of increase (λ)	204	$y = 1.8511(0.2495) - 0.1339(0.0302)T + 0.0069(0.0012)T^2 - 0.0001(0.0000)T^3$

All models included a third order term of temperature, but only significant terms ($p < 0.001$) were included in the final model

All models were highly significant ($p < 0.001$). See Table 1 for more details. n is the number of observations

[a] The link function relates y to the expected value of the response variable. Values in parentheses give standard errors of the estimated parameters

[b] Link-function is the logarithmic function. Back-transformed values are obtained as $y^* = e^y$

[c] Link-function is the logit function. Back-transformed values are obtained as $y^* = e^y/(1 + e^y)$
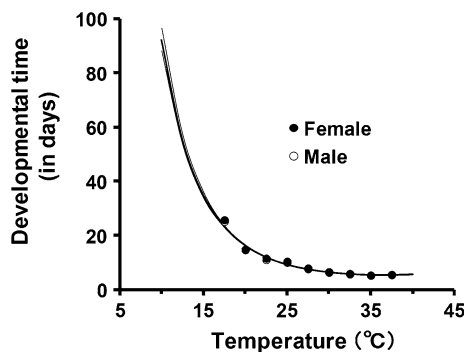

Fig. 1 Effect of temperature and/or sex on the developmental period from egg to adult in *Tetranychus macfarlanei* at various temperatures. See Appendix 1 for further information. *Points* show the sample averages with 95% confidence limits. The *heavy line* shows the predictions based on the generalized linear models after eliminating non-significant terms. *Thin lines* show the 95% confidence limits for the predicted line. The models as well as total sample sizes are given in Table 2

Table 3 Estimated values of constants in linear and non-linear models describing the relationship between temperature (°C) and developmental rates in *Tetranychus macfarlanei* on bean leaf discs

Stage	Law of total effective temperature linear model			
	$t \pm$ SE	$k \pm$ SE	r^2	Linear-model equation
Egg-to-female adult	12.88 ± 0.37	115.99 ± 4.69	0.9962	$y = 0.0086x - 0.1111$
Egg-to-male adult	12.86 ± 0.38	110.85 ± 4.63	0.9927	$y = 0.0090x - 0.1160$
Egg-to-egg	12.98 ± 0.37	125.32 ± 5.16	0.9963	$y = 0.0080x - 0.1036$

Stage	Thermodynamic non-linear model (SSI model)								
	$[T_\phi]$ (K)	T_ϕ (°C)	ρ	ΔH_A (cal/mol)	ΔH_L (cal/deg mol)	ΔH_H (cal/deg mol)	$[T_L]$ (K)	$[T_H]$ (K)	χ^2
Egg-to-female adult	297.55	24.40	0.0993	15,348	−61,953	52,449	286.03	311.81	0.00211
Egg-to-male adult	297.54	24.39	0.1040	15,293	−61,967	53,116	286.01	311.66	0.00238
Egg-to-egg	297.35	24.20	0.0895	15,416	−63,919	51,706	286.13	311.71	0.00220

t: lower threshold temperature (°C), k: thermal constant (°C), T_ϕ: intrinsic optimum temperature (°C), ρ: development rate at T_ϕ, ΔH_A: enthalpy of activation, ΔH_L and ΔH_H: change in enthalpy associated with low and high temperature inactivation of enzymes, respectively, T_L and T_H: temperature at which an enzyme is half active, below and above the optimum temperature, respectively
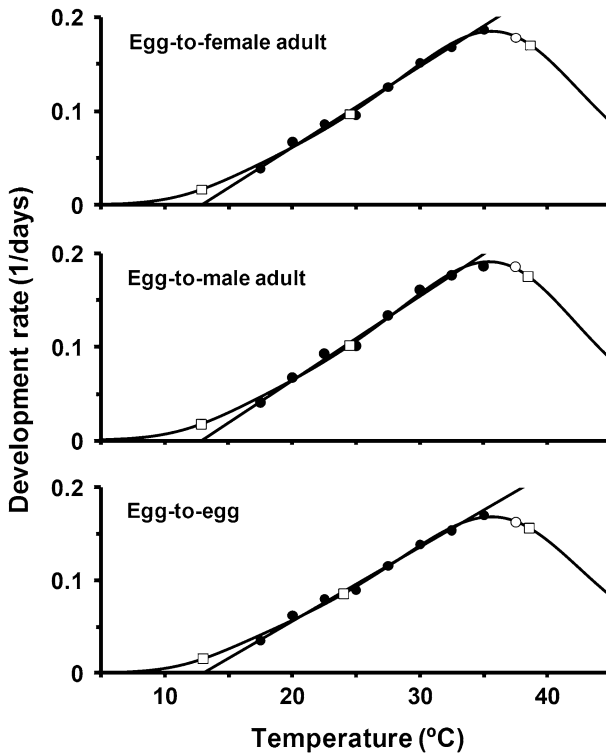
Fig. 2 Ikemoto and Takai's (2000) linear and thermodynamic (non-linear) SSI models fitted to the temperature-dependent development of *Tetranychus macfarlanei*. *Circles* show data points. *Open circles* indicate data points outside the range of the linear model. *Lower squares* show T_L (=t), *middle squares* show intrinsic optimum temperature (T_Φ), and *upper squares* are T_H of constant estimated by non-linear model (see also Table 3)

17.5°C. Mean generation time (t_G) and doubling time (t_D) decreased with increasing temperatures: t_G ranged from 37.0 days at 17.5°C to 9.5 days at 35°C. Likewise, t_D declined from 6.8 days at 17.5°C to 1.6 days at 35°C (Appendix 4).

Discussion

Temperature had a highly significant effect on the development and reproduction of *T. macfarlanei*. Our results demonstrate that *T. macfarlanei* was capable of producing offspring across a wide range of temperatures. We found that temperatures higher than 35°C have a detrimental effect on the development and survival. Although 73.3–90.6% of immatures reached adulthood at temperatures ranging from 17.5 to 35°C, immature survival declined to 62.5% at 37.5°C. Changes in lipids, rate imbalances, perturbation of ionic activities, as well as desiccation have been identified as possible mechanisms of arthropod death due to high temperatures. It is also possible that at higher temperatures the arthropods were unable to replace the loss of water from their body, leading to higher mortality (Fields 1992). Ullah et al. (2011) showed that mortality of *T. kanzawai* and *T. merganser* increased sharply at temperatures higher than 35°C and a similar trend was also observed

Fig. 3 Effect on temperature on mean durations of oviposition period, female longevity and total fecundity in *Tetranychus macfarlanei*. See Appendix 2 for further information. *Points* show the sample averages with 95% confidence limits. The *heavy lines* show the predictions based on the generalized linear models after eliminating non-significant terms. *Thin lines* show the 95% confidence limits for the predicted line. The models as well as total sample sizes are given in Table 2
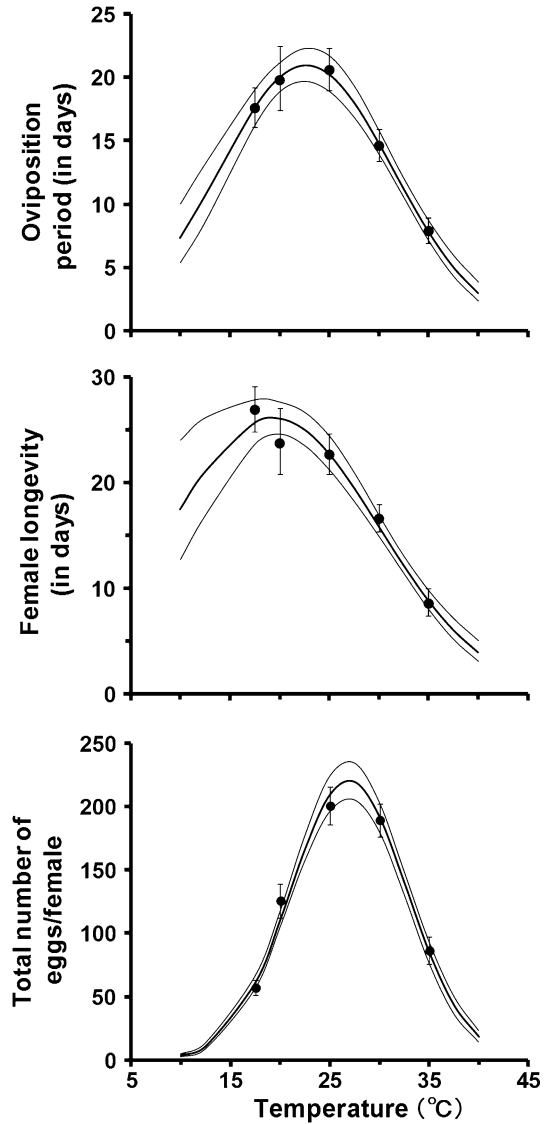
in *T. tumidus* (Liu and Tsai 1998). In the latter species, survival rates at 15 to 30°C were higher than 78.4%, but at 35°C, it was reduced to 56.4%. Insects have an optimum temperature range for development (Huffaker et al. 1999; Huang et al. 2008). Our results indicate that most *T. macfarlanei* eggs could not hatch at 15 and 40°C, and larval mortality reached 100% at both temperatures.

Development rate of *T. macfarlanei* increased almost linearly with an increase in temperature to 35°C, but did not increase further at higher temperature (37.5°C; Fig. 2). Similar trends were reported for other *Tetranychus* species such as *T. tumidus* (Liu and Tsai 1998), *T. mcdanieli* (Roy et al. 2003), *T. evansi* (Gotoh et al. 2010), *T. kanzawai* and *T. merganser* (Ullah et al. 2011). An excellent fit was obtained by Ikemoto and Takai's (2000) linear model for egg-to-adult (female and male) and egg-to-egg development of
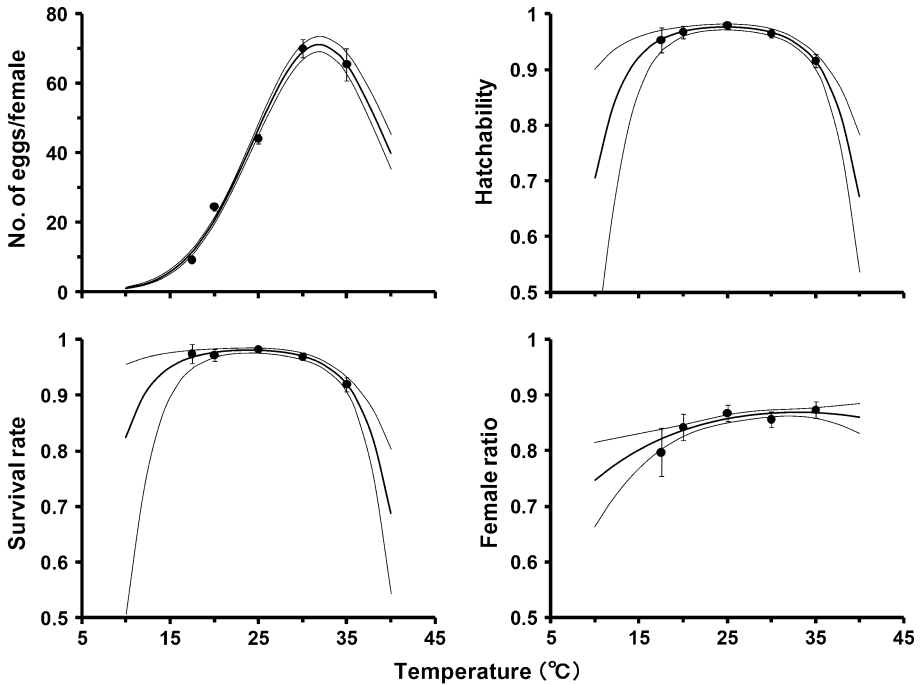
Fig. 4 Temperature effects on (*top left*) number of eggs laid per female during the first five days of oviposition, (*top right*) hatch rate from eggs to larvae, (*bottom left*) survival rate from hatching to the adult stage, and (*bottom right*) offspring sex ratio expressed as proportion. *Points* show the sample averages with 95% confidence limits. The *heavy lines* show the predictions based on the generalized linear models after eliminating non-significant terms. *Thin lines* show the 95% confidence limits for the predicted line. The models as well as total sample sizes are given in Table 2

T. macfarlanei, based on the obtained coefficient of determination ($0.993 \leq r^2 \leq 0.996$). In many temperature-dependent development studies of arthropods linear models were used to estimate the lower thermal threshold and the thermal constant (Howell and Neven 2000). Lower thermal threshold and thermal constant of an insect are indicators for forecasting its potential distribution and abundance (Campbell et al. 1974; Huang et al. 2008). The estimated lower thermal threshold (*t*) of *T. macfarlanei* was 12.9°C for egg-to-adult development (both female and male) (Table 3). The *t* value of *T. macfarlanei* is very close to that of seven strains of *T. evansi* (11.9–12.5°C; Gotoh et al. 2010) and *T. merganser* (12.2–12.3°C; Ullah et al. 2011), but slightly higher than that of *T. okinawanus* (11.6°C; Takafuji et al. 1996) and *T. tumidus* (11.9°C; Liu and Tsai 1998), which occur all in tropical and subtropical regions. In contrast, the *t* value of *T. macfarlanei* is higher than that of *T. urticae* (10.0 and 10.5°C; Herbert 1981; Bounfour and Tanigoshi 2001), *T. pueraricola* (10.8°C; Gotoh et al. 2004) and *T. kanzawai* (10.8°C; Ullah et al. 2011), which mainly occur in the temperate region. Tetranychid mites might escape the adverse temperature condition in winter of temperate regions by entering diapause, but as far as known *T. macfarlanei* has no diapause ability (Jose and Shah 1989). Therefore, temperate regions seem unsuitable for the development of *T. macfarlanei*.

We found that oviposition period and adult longevity of *T. macfarlanei* declined with increasing temperatures. Our results agree with the work of Bonato (1999) and Ullah et al. (2011), who observed that the oviposition period and adult longevity of *T. evansi*,
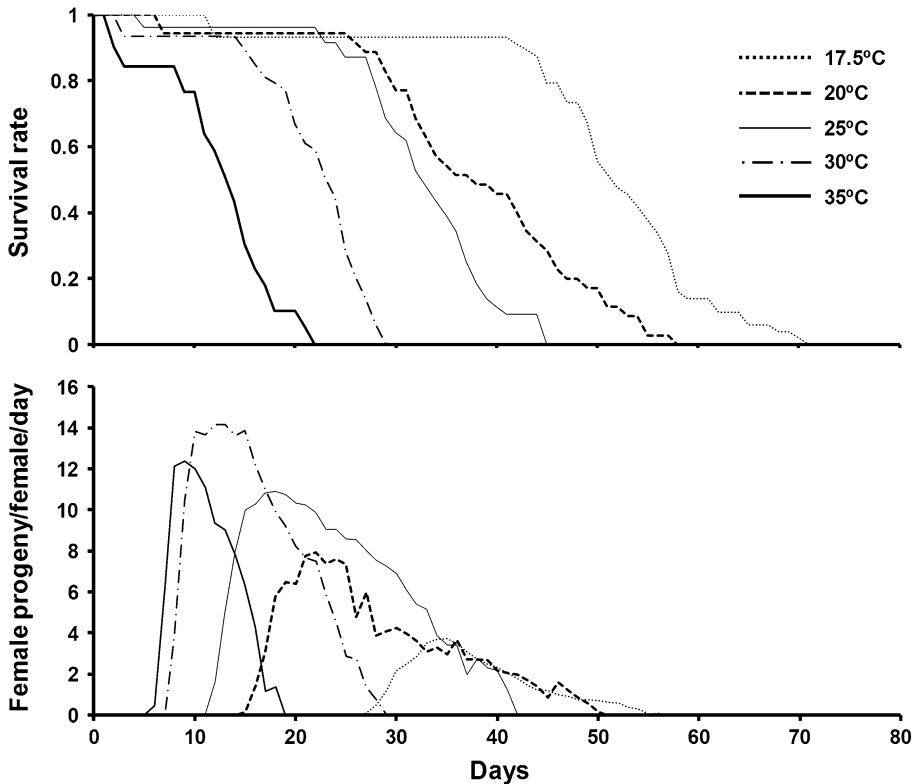
Fig. 5 Age-specific survival rate (l_x *top*) and age-specific fecundity rate (m_x *bottom*) of *Tetranychus macfarlanei* females at different temperatures

T. merganser and *T. kanzawai* decreased in response to temperature increase. They found that lower temperatures extended the duration of the egg-laying period, which could be explained by reduced activity, less energy used for reproduction, or both (Papaj 2000; Carey 2001; Jervis et al. 2005, 2007; Berger et al. 2008). Fecundity was highest at 25–30°C. The lowest fecundity was obtained at 17.5°C followed by 35°C, which may indicate adverse effects of low and high temperatures on the biological processes of *T. macfarlanei* and explain why this species is prevalent in a wider part of the world.

Sabelis (1991) reviewed tetranychid life-table parameters and reported that r_m-values for *Tetranychus* mites ranged from 0.219 to 0.336 day^{-1} near 25°C. The r_m-value of *T. macfarlanei* falls within this range (0.275 day^{-1}). The r_m-value of *T. macfarlanei* was somewhat higher than that for *T. cinnabarinus* (0.164 day^{-1}; Hazan et al. 1973), *T. mcdanieli* (0.201 day^{-1}; Tanigoshi et al. 1975), *T. tumidus* (0.232 day^{-1}; Liu and Tsai 1998), *T. evansi* (0.243 day^{-1}; Bonato 1999) and *T. marianae* (0.172 day^{-1}; Noronha 2006) at 25 ± 1°C, and it was similar to the r_m-value reported for *T. desertorum* (0.28–0.29 day^{-1}; Nickel 1960), *T. evansi* (0.264–0.277 day^{-1}; Gotoh et al. 2010), *T. kanzawai* (0.187–0.283 and 0.282 day^{-1}; Gotoh and Gomi 2003 and Ullah et al. 2011, respectively) and *T. merganser* (0.279 day^{-1}; Ullah et al. 2011). The similarities of the r_m-values between *T. macfarlanei* and other *Tetranychus* species suggest that *T. macfarlanei* has equal
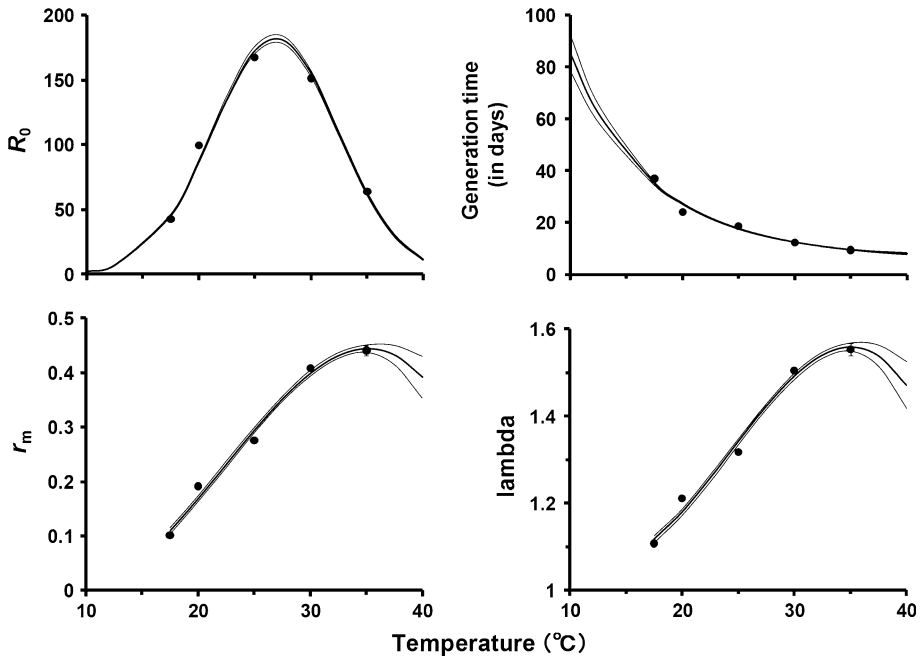
Fig. 6 Effect of temperature on demographic parameters of *Tetranychus macfarlanei*. See Appendix 4 for further information. R_0, net reproductive rate (*top left*); r_m, intrinsic rate of natural increase (*bottom left*); t_G, mean generation time (*top right*); λ, finite rate of increase (*bottom right*). The *heavy lines* for R_0 and r_m show the predictions, based on the generalized linear models after eliminating non-significant terms. *Thin lines* show the 95% confidence limits for the predictions. The models as well as total sample sizes are given in the Table 2

potential as *T. desertorum*, *T. evansi*, *T. kanzawai* or *T. merganser* to damage a variety of crops.

This study described the temperature-dependent development of the *T. macfarlanei* Bangladeshi strain under the broad range of temperatures generally prevailing in this region, and estimated its key bioclimatic parameters. Quantification of the thermal response of *T. macfarlanei* in a demographic context is critical for describing its population dynamics, and it may promote the understanding of adaptation to climatic conditions and predict how quickly its densities may change over time. The information gathered in this study will be important in the management of *T. macfarlanei*, by providing a better understanding of its life-table parameters and its ability to survive under different temperature regimes.

Appendix 1

See Table 4.

Table 4 Developmental duration (days ± SE) from egg to adult and preoviposition period (days ± SE) and percentage (%) of immature survival (egg to adult) of *Tetranychus macfarlanei* on bean leaf discs at various temperatures under a 16L:8D photoperiod

Temperature (°C)		N^a	Egg	Larva	Proto-chrysalis	Proto-nymph	Deuto-chrysalis	Deuto-nymph	Teleio-chrysalis	Egg-to-adult	Preoviposition period	% Immature survival
17.5	♀	58	12.60 ± 0.07	2.41 ± 0.07	2.07 ± 0.04	1.91 ± 0.04	1.98 ± 0.02	2.36 ± 0.06	2.41 ± 0.08	25.76 ± 0.12	3.00 ± 0.08	79.2 [96][b]
	♂	18	11.72 ± 0.21	2.17 ± 0.09	2.00 ± 0.08	2.00 ± 0.08	2.06 ± 0.04	2.28 ± 0.04	2.22 ± 0.10	24.44 ± 0.25		
20	♀	54	6.94 ± 0.04	1.33 ± 0.07	1.42 ± 0.07	1.11 ± 0.04	1.19 ± 0.05	1.19 ± 0.05	1.76 ± 0.06	14.89 ± 0.09	1.26 ± 0.06	89.6 [96]
	♂	32	7.09 ± 0.09	1.44 ± 0.10	1.56 ± 0.10	0.81 ± 0.07	1.31 ± 0.08	1.03 ± 0.06	1.53 ± 0.09	14.78 ± 0.13		
22.5	♀	52	5.42 ± 0.07	0.96 ± 0.03	0.92 ± 0.04	0.81 ± 0.04	1.08 ± 0.04	1.00 ± 0.00	1.40 ± 0.07	11.60 ± 0.07	0.88 ± 0.04	85.2 [108]
	♂	40	5.60 ± 0.08	0.80 ± 0.06	0.80 ± 0.06	0.78 ± 0.07	0.93 ± 0.04	0.88 ± 0.05	0.95 ± 0.04	10.73 ± 0.07		
25	♀	52	4.65 ± 0.07	0.88 ± 0.05	0.87 ± 0.05	0.69 ± 0.07	1.00 ± 0.03	0.98 ± 0.03	1.38 ± 0.07	10.46 ± 0.08	0.75 ± 0.06	90.6 [96]
	♂	35	5.00 ± 0.00	0.69 ± 0.08	0.83 ± 0.07	0.60 ± 0.08	0.97 ± 0.03	0.69 ± 0.08	1.09 ± 0.06	9.86 ± 0.08		
27.5	♀	57	3.52 ± 0.01	0.72 ± 0.03	0.76 ± 0.04	0.67 ± 0.03	0.61 ± 0.03	0.88 ± 0.03	0.81 ± 0.03	7.96 ± 0.05	0.71 ± 0.03	83.0 [112]
	♂	36	3.65 ± 0.04	0.67 ± 0.04	0.67 ± 0.04	0.50 ± 0.04	0.63 ± 0.04	0.71 ± 0.04	0.64 ± 0.04	7.46 ± 0.08		
30	♀	58	3.05 ± 0.02	0.61 ± 0.03	0.57 ± 0.02	0.50 ± 0.01	0.51 ± 0.01	0.66 ± 0.33	0.71 ± 0.03	6.61 ± 0.04	0.62 ± 0.03	83.9 [112]
	♂	36	3.24 ± 0.04	0.46 ± 0.03	0.51 ± 0.01	0.40 ± 0.03	0.50 ± 0.00	0.50 ± 0.00	0.58 ± 0.03	6.19 ± 0.05		
32.5	♀	58	2.53 ± 0.02	0.67 ± 0.03	0.53 ± 0.02	0.46 ± 0.04	0.51 ± 0.02	0.53 ± 0.02	0.72 ± 0.03	5.95 ± 0.06	0.57 ± 0.02	84.8 [112]
	♂	37	2.87 ± 0.04	0.43 ± 0.03	0.45 ± 0.03	0.45 ± 0.03	0.50 ± 0.00	0.49 ± 0.01	0.47 ± 0.03	5.65 ± 0.04		
35	♀	53	2.44 ± 0.02	0.57 ± 0.04	0.35 ± 0.04	0.50 ± 0.00	0.50 ± 0.00	0.50 ± 0.01	0.50 ± 0.00	5.36 ± 0.06	0.54 ± 0.02	73.3 [120]
	♂	35	2.56 ± 0.03	0.54 ± 0.02	0.46 ± 0.02	0.33 ± 0.04	0.50 ± 0.02	0.44 ± 0.03	0.53 ± 0.02	5.36 ± 0.04		
37.5	♀	55	2.46 ± 0.01	0.55 ± 0.01	0.50 ± 0.00	0.49 ± 0.01	0.50 ± 0.00	0.51 ± 0.01	0.61 ± 0.02	5.61 ± 0.02	0.55 ± 0.02	62.5 [144]
	♂	35	2.59 ± 0.02	0.54 ± 0.03	0.47 ± 0.01	0.33 ± 0.03	0.44 ± 0.02	0.46 ± 0.02	0.54 ± 0.02	5.37 ± 0.06		

[a] Number of individuals tested

[b] Number of eggs tested

Appendix 2

See Table 5.

Table 5 Mean duration (days ± SE) of adult phases and longevity, and oviposition rates (avg ± SE) in *Tetranychus macfarlanei* on bean leaf discs at four temperatures under a 16L:8D photoperiod

Temperature (°C)	N^a	Oviposition	Post-oviposition	Female longevity	Total eggs/female	Eggs/♀/day
17.5	47	18.36 ± 0.79	6.68 ± 0.86	27.89 ± 1.10	56.98 ± 2.93	3.14 ± 0.10
20	34	21.09 ± 1.29	3.00 ± 0.79	25.35 ± 1.56	125.68 ± 6.58	6.10 ± 0.12
25	43	21.23 ± 0.76	1.47 ± 0.29	23.44 ± 0.91	200.49 ± 7.44	9.45 ± 0.11
30	47	15.19 ± 0.58	0.94 ± 0.22	17.11 ± 0.58	189.21 ± 6.44	12.66 ± 0.63
35	33	8.33 ± 0.45	0.85 ± 0.32	9.30 ± 0.64	86.27 ± 5.33	10.25 ± 0.25

[a] Number of females tested

Appendix 3

See Table 6.

Table 6 Number of eggs laid during the first 5 days of the oviposition period, hatchability of eggs, survival rate of immature stages and the proportion of females reaching adulthood (avg ± SE) of *Tetranychus macfarlanei* on bean leaf discs at five temperatures under a 16L:8D photoperiod

Temperature (°C)	N^a	No. of eggs laid	% Hatch	% Survival	% Female
17.5	47	9.26 ± 0.22	95.67 ± 0.93	97.41 ± 0.77	80.17 ± 0.95
20	40	24.58 ± 0.52	96.87 ± 0.52	97.35 ± 0.45	84.27 ± 0.51
25	44	44.09 ± 0.64	98.01 ± 0.33	98.17 ± 0.33	86.78 ± 0.45
30	38	70.03 ± 1.29	96.57 ± 0.58	96.75 ± 0.58	85.57 ± 0.48
35	32	65.50 ± 2.26	91.69 ± 0.72	91.95 ± 0.78	87.73 ± 0.74

[a] Number of females tested

Appendix 4

See Table 7.

Table 7 Demographic parameters (avg ± SE) of *Tetranychus macfarlanei* on bean leaf discs at five temperatures under a 16L:8D photoperiod: net reproductive rate (R_0), intrinsic rate of natural increase (r_m, day^{-1}), mean generation time (t_G, day), finite rate of increase (λ), doubling time (t_D, day)

Temperature (°C)	N^a	R_0	r_m	t_G	λ	t_D
17.5	47	42.57 ± 0.05	0.1018 ± 0.0015	37.04 ± 0.32	1.1072 ± 0.0009	6.84 ± 0.06
20	34	99.58 ± 0.16	0.1916 ± 0.0018	24.05 ± 0.15	1.2112 ± 0.0014	3.62 ± 0.02
25	43	167.40 ± 0.15	0.2753 ± 0.0023	18.62 ± 0.09	1.3170 ± 0.0018	2.52 ± 0.01
30	47	151.27 ± 0.12	0.4088 ± 0.0044	12.30 ± 0.08	1.5052 ± 0.0037	1.70 ± 0.01
35	33	63.82 ± 0.12	0.4407 ± 0.0068	9.46 ± 0.10	1.5543 ± 0.0071	1.58 ± 0.02

[a] Number of females tested

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