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Development and reproduction of five *Tetranychus* species (Acari: Tetranychidae): Do they all have the potential to become major pests?

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Abstract The objective of this study was to investigate whether four spider mite species, *Tetranychus ludeni*, *T. phaselus*, *T. piercei* and *T. truncatus*, currently with insignificant economic impact, have the potential to achieve the same status as *T. urticae*, which until now has been considered as the most serious tetranychid pest species in orchards and greenhouses. We investigated the effect of temperature on development, survival and oviposition at 11 constant temperatures ranging from 15 to 40 °C at intervals of 2.5 °C and estimated demographic parameters, such as the intrinsic rate of natural increase (r_m), for these five species at five constant temperatures. Developmental time from egg to adult (female and male) decreased with increasing temperature from 15 to 32.5 °C in all five species, but increased slightly at 35 °C or higher, especially in *T. ludeni* and *T. urticae*. Using linear and non-linear developmental rate models, the lower thermal thresholds for egg-to-adult (female and male) and egg-to-egg development were found to range from 9.8 to 11.7 and from 9.8 to 11.4 °C, respectively. The intrinsic optimal temperature (T_Φ) ranged from 18.0 to 27.4 °C for egg-to-female adult and from 23.9 to 27.2 °C for egg-to-egg development. The oviposition period and adult longevity were strongly affected by temperature. The r_m-values increased with increasing temperature from 15 to 30 or 35 °C in all five species. The highest r_m-values at each temperature were 0.114 day^{-1} at 15 °C for *T. ludeni*, 0.199 day^{-1} at 20 °C for *T. urticae*, 0.314 day^{-1} at 25 °C for *T. ludeni*, 0.451 day^{-1} at 30 °C for *T. ludeni* and 0.433 day^{-1} at 35 °C for *T. truncatus*. The total fecundity, net reproductive rate (R_0) and r_m of *T. ludeni* were higher than those of *T. urticae* at all temperatures. *T. piercei* and *T. truncatus* showed higher r_m-values at 30 and

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35 °C than *T. urticae*. The results indicate that the former three species are better adapted to hot weather than *T. urticae* and have a high potential to become serious pests.

Keywords *Tetranychus ludeni* · *T. phaselus* · *T. piercei* · *T. truncatus* · *T. urticae* · Thermal threshold · Intrinsic rate of natural increase

Introduction

There are many studies showing a change in mite species composition in fruit tree orchards taking place during the past 50 years in Japan. Thus, in pear orchards, *Amphitetranychus viennensis* (Zacher), which was dominant until the 1960s, was replaced with *Tetranychus urticae* Koch (green form, G) and/or *Tetranychus kanzawai* Kishida (Nakagaki 1980; Uchida 1982; Takafuji and Kamibayashi 1984; Gotoh 1997; Kishimoto 2002). In apple orchards, *Panonychus ulmi* (Koch), which was a dominant species until 1950s, was displaced by *T. urticae* (G) (Fujibayashi and Kushida 1992). However, after using sex pheromone for disrupting the mating of fruit borers and leaf rollers application of pesticides has been drastically reduced and as a result natural enemies of spider mites began to increase and to effectively control *T. urticae* (G). Recently, previously dominant species, such as *A. viennensis* and *P. ulmi*, have increased again to become dominant instead of *T. urticae* (Okazaki 2000). These observations are experimentally confirmed in pear orchards, where agrochemical use was artificially managed: *A. viennensis* was dominant in agrochemical-free orchards, *Panonychus citri* (McGregor) was dominant in pesticide-free orchards, and *T. urticae* (G) was dominant in conventionally controlled orchards (Kishimoto 2002). Such changes in species composition are attributed to the negative effects of agrochemicals on the natural enemies attacking *Tetranychus* species and to the ability of spider mites to develop resistance against agrochemicals (van de Vrie et al. 1972; Trichilo and Wilson 1993; Goka 1999; Takafuji et al. 2000). On the other hand, tarsonemid mites have gradually become more serious pests after integrated pest management programs have been introduced in greenhouse crops (Mizukoshi and Goto 2003). Tarsonemid mites such as *Phytonemus pallidus* (Banks) and *Polyphagotarsonemus latus* (Banks) had once been simultaneously controlled with agrochemicals sprayed for controlling tetranychid mites and small insect pests as a side-effect, but recently application of insecticides and acaricides has been abandoned or reduced in order to protect the commercially produced natural enemies released for controlling spider mites and small insect pests. The enemies are *Phytoseiulus persimilis* Athias-Henriot, *Neoseiulus californicus* (McGregor) and *Amblyseius swirskii* Athias-Henriot. This indicates that a reduction in the use of agrochemicals can lead to an increase in minor or cryptic pests. Consequently, changes in the application of agrochemicals such as the number of sprayings or the chemical components applied (e.g., shifts from chemicals having broader spectrum to ones having target-specificity or a narrower spectrum) may influence spider mite composition in a field. This suggests that minor spider mite species (i.e., species that are usually not regarded as pests) inhabiting orchards and greenhouses, or neighboring areas, might become more dominant in environments with relatively low impact of agrochemicals, even if the mites have not yet developed resistance to such chemicals. However, the effect of agrochemicals on the minor species, the preference of natural enemies for minor species and the potential capacity of minor species for population increase at different temperatures remain unknown.

Preliminary observations have shown that *Tetranychus ludeni* Zacher, usually considered a minor pest in Japan, sometimes has outbreaks in commercial green pepper fields with ongoing IPM programs. Likewise, in Inner Mongolia, China, outbreaks of *Tetranychus truncatus* Ehara occur in corn cultivated without using any agrochemicals (Gotoh, personal observation). Therefore, the purpose of this study was to find out whether minor *Tetranychus* species have the potential to become important pests. We investigated the effect of temperature on development and demographic parameters of four minor species of the genus *Tetranychus* in Japan, and compared the values with those obtained for the serious pest, *T. urticae* (G), which was also included in this study. *Tetranychus urticae* is known as one of the most important pests on many crops worldwide. It attacks more than 1000 plant species, including vegetables, fruit trees and ornamentals (Bolland et al. 1998; Migeon and Dorkeld 2006–2013). Of the 13 *Tetranychus* species found in Japan, *Tetranychus okinawanus* Ehara and *Tetranychus neocaledonicus* Andre do not occur at the main island of Japan, Honshu, whereas *Tetranychus ezoensis* Ehara only infests coniferous trees. Life histories of *Tetranychus parakanzawai* Ehara and *Tetranychus pueraricola* Ehara & Gotoh have been studied by Gotoh and Gomi (2003) and Gotoh et al. (2004), respectively. *Tetranychus mismaiensis* Ehara & Gotoh is extremely rare in Japan and has only been collected once at Hokkaido, northern Japan. *Tetranychus urticae*, *T. kanzawai* and *Tetranychus evansi* Baker & Pritchard are all serious pests (Bolland et al. 1998). The remaining four species, currently regarded as minor pests, are *T. ludeni*, *Tetranychus phaselus* Ehara, *Tetranychus piercei* McGregor and *T. truncatus*. They have been found at least once at the main island, Honshu, where they infested a crop and/or occurred on weeds growing in or close to a field crop. However, biological information about the species is still scarce. *Tetranychus ludeni* occurs worldwide and infests more than 250 plant species. The species does not have diapause ability and all stages can be found throughout a year. Takafuji (1980) found three distinct population peaks (in June, August and November) on goldenrod, *Solidago altissima* L. *Tetranychus phaselus* is distributed within an area encompassing East Russia, China, Japan, Korea and Taiwan and appears on about ten plant species. *Tetranychus piercei* is known from south-eastern Asia and appears on about 30 plant species (Bolland et al. 1998). *Tetranychus truncatus* is known from Asia and infests more than 60 plant species. This is an extremely rare species in Japan, but it is a very severe pest on various crops such as corn, soybean, eggplant and cucumber in Thailand (Sakunwarin et al. 2003) and China (Pang et al. 2004). There are several studies

Table 1 Collection data of five *Tetranychus* species used in this study

Species	Locality	Latitude	Longitude	Date	Host plant
T. ludeni Zacher	Ami, Ibaraki, Japan	36°04′N	140°21′E	17 Oct 1995	*Solidago altissima* L.
T. phaselus Ehara	Ushiku, Ibaraki, Japan	35°97′N	140°18′E	29 June 2000	*Glycine max* L.
T. piercei McGregor	Shinoyama, Hyogo, Japan	35°04′N	135°13′E	26 Sept 2009	*Glycine max* L.
T. truncatus Ehara	Syugakuin, Kyoto, Japan	35°05′N	135°79′E	8 May 2004	*Solanum nigrum* L.
T. urticae Koch (G)[a]	Takikawa, Hokkaido, Japan	43°56′N	141°90′E	16 July 2001	*Citrullus lanatus* (Thunb.)

[a] Green form

on its life-history parameters (Sakunwarin et al. 2003; Pang et al. 2004) and its development at different temperatures, i.e., lower thermal threshold (Chao and Lo 1974; Fan et al. 2003; Sakunwarin et al. 2003).

Materials and methods

Mites

Table 1 summarizes information about the five *Tetranychus* species used in this study. Each species was maintained separately on down-side-up leaf discs (ca. 16 cm^2) of common bean (*Phaseolus vulgaris* L.) placed on water-saturated polyurethane mats in plastic dishes (90 mm diameter, 20 mm depth) and kept at 25 ± 1 °C and under a 16:8 h light:dark photoperiod with 60–70 % relative humidity. Cultures of the five species had been kept under the same laboratory conditions for some years prior to the experiments which took place in 2010.

Immature development

Inseminated adult females obtained from the stock cultures of each species were transferred individually onto a leaf disc (2 × 2 cm) of common bean and kept at one of 11 constant temperatures, ranging from 15 to 40 °C with intervals of 2.5 °C, 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 egg hatching rate and the survival rate, but were excluded from the calculation of developmental time.

Reproduction and female longevity

When a female teleiochrysalis appeared in the developmental experiments, two adult males obtained from the stock cultures were introduced onto the leaf disc (2 × 2 cm) for mating and then removed 48 h after emergence of the adult female as previous experiments have shown that females of the five species only mate once during lifetime (Gotoh unpubl). 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 15, 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 lifetime 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 at 1 to 2-week intervals using a fine brush.

Hatchability, survivability and sex ratio

To calculate age-specific survival rate (l_x) and fecundity rate (m_x) at 15, 20, 25, 30 and 35 °C, it was necessary to assess (1) egg hatchability, (2) the survival rate of immature stages and (3) the proportion of female offspring. To obtain these data, single female teleiochrysales were placed with two adult males on a leaf disc (ca. 16 cm^2) of common bean for copulation. The females were allowed to lay eggs for 5 days after the pre-oviposition period. The eggs obtained from each female were kept to determine the above-mentioned parameters after reaching adulthood. As discussed by Sabelis (1981), the sex ratio of *T. urticae* gets increasingly female-biased within the first 5–6 days of egg laying. Though older females may tend to produce more female eggs than younger females (see also Riahi et al. 2011), it is not likely to affect the life-table parameters markedly as the majority of eggs are produced when the females are still young. Especially the intrinsic rate of natural increase (r_m) depends on survival and fecundity rates during early ages (Birch 1948). We therefore consider the sex ratio determined on basis of eggs produced during the first 5–6 days of egg-laying as the most representative for the species in focus.

Life-table parameters

The r_m, which expresses the maximum innate capacity of increase of a population living under optimal conditions, was estimated from the life-fecundity table according to the equation given by Birch (1948): $\sum_{x=0}^{\infty} l_x m_x e^{-r_m x} = 1$, where x is age in days, l_x is the age-specific survival rates of females [(the fraction 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). The net reproductive rate (R_0) was calculated as $R_0 = \sum_{x=0}^{\infty} l_x m_x$, the mean generation time (t_G) in days as $t_G = \ln R_0/r_m$, the finite rate of increase (λ) as $\lambda = e^{r_m}$, and the doubling time (t_D) in days as $t_D = (\ln 2)/r_m$.

We also calculated r_m by means of the approximate method suggested by Wyatt and White (1977) using the total number of eggs produced per female from day d to day D (M_d), where d is the duration of the preoviposition period at a given temperature and $D = 2d$. Thus, r_m was estimated as $r_m = c \ln M_d / d$ where c is a species specific correction factor equal to 0.749 for mites (Wyatt and White 1977). The BCaWW method (bias corrected and accelerated bootstrap) was used to calculate 95 % confidence intervals for r_m obtained by means of Wyatt and White's method (see also Lawo and Lawo 2011; the values were calculated based on their procedure using free R software).

Effect of temperature on mite developmental rate

Developmental rates (calculated as 1/developmental duration) at different temperatures were used in linear and non-linear models. The thermal constant and lower thermal threshold were determined using the line-fitting method proposed by Ikemoto and Takai (2000). As the method assumes a linear increase in developmental rate with temperature, we excluded data obtained at temperatures above 30 °C from the analysis. The linear model by Ikemoto and Takai (2000) fitted to data is given as:

$$\frac{1}{D} = -\frac{t}{k} + \frac{1}{k}T \qquad (1)$$

where D is the duration of development (days), T is environmental temperature (°C), t is the lower thermal threshold and k is the thermal constant.

The non-linear thermodynamics model describes the developmental rate over a wider range of temperatures and allows for estimating the 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):

$$r([T]) = \frac{\rho \frac{[T]}{[T_\Phi]} \exp\left\lfloor \frac{\Delta H_A}{R}\left(\frac{1}{[T_\Phi]} - \frac{1}{[T]}\right)\right\rfloor}{1 + \exp\left[\frac{\Delta H_L}{R}\left(\frac{1}{[T_L]} - \frac{1}{[T]}\right)\right] + \exp\left[\frac{\Delta H_H}{R}\left(\frac{1}{[T_H]} - \frac{1}{[T]}\right)\right]} \tag{2}$$

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:

$$[T_\Phi] = \frac{\Delta H_L - \Delta H_H}{R \ln\left(-\frac{\Delta H_L}{\Delta H_H}\right) + \left(-\frac{\Delta H_L}{[T_L]}\right) - \left(-\frac{\Delta H_H}{[T_H]}\right)} \tag{3}$$

The SSI model was modified and developed as SSI-P, which runs on R statistical software by Shi et al. (2011). Finally, Ikemoto et al. (2013) improved their model and developed the program OptimSSI-P, which estimates T_Φ along with its confidence limit.

Statistical analysis

Data were analyzed by means of analysis 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, intrinsic rate of natural increase, generation time and the finite rate of increase), and predictor variables, such as gender (G), temperature (T) and species (S), in order to identify which of the predictor variables contribute most to explain the variation in data. The full ANCOVA model for analysing all response variables includes the main effects of species (with five levels), gender (with two levels) and temperature (T and T^2) as well as all their first- and second-order interactions. Thus, the full model predicting egg-to-adult development has 30 parameters of which one expresses the intercept (denoted β_0) and the remaining 29 are associated with the predictor variables. The full model for the remaining response variables does not include gender and has therefore only 14 parameters plus β_0. In some instances, the model also involved third-order terms of temperature, but only the significant terms were included in the final model.

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

Table 2 Results of the statistical analyses based on PROC GENMOD for analyzing all response variables of five *Tetranychus* species

Response variable	Distribution	Link function	N	Null model[a]	Full model[b]	
				Deviance	Deviance	Effect of all factors
Egg-to-adult development	Normal[f]	Identity	3101	879.1	26.59	$F_{29,3071} = 3395.6$***
Eggs/female for 5 days oviposition	Poisson	Logarithmic	538	8145.8	888.7	$F_{14,523} = 305.1$***
Hatch rate for 5 days oviposition	Binomial	Logit	538	1516.6	686.6	$F_{14,523} = 45.2$***
Juv. survival rate for 5 days oviposition	Binomial	Logit	538	2098.7	1010.4	$F_{14,523} = 40.2$***
Sex ratio for 5 days oviposition	Binomial	Logit	538	558.5	431.1	$F_{14,523} = 11.0$***
Oviposition period	Normal[f]	Identity	722	425.8	90.84	$F_{14,707} = 186.2$***
Adult longevity	Normal[f]	Identity	722	402.3	74.58	$F_{14,707} = 221.9$***
Total fecundity/female	Poisson	Logarithmic	722	28,048.2	7827.5	$F_{14,707} = 130.5$***
Net reproduction rate (R_0)	Normal[f]	Identity	722	356.8	19.7	$F_{14,707} = 865.1$***
Intrinsic rate of increase (r_m)	Normal	Identity	722	9.94	1.20	$F_{14,707} = 367.6$***
Mean generation time (t_G)	Normal	Identity	722	110,172.5	4517.0	$F_{14,707} = 1181$***

Response variable	Full model excl. temperature[c]		Full model excl. species[d]		Full model excl. gender[e]	
	Deviance	Effect of temperature	Deviance	Effect of species	Deviance	Effect of gender
Egg-to-adult development	856.3	$F_{20,3071} = 148.8$***	42.63	$F_{24,3071} = 48.2$***	27.89	$F_{15,3071} = 9.40$***
Eggs/female for 5 days oviposition	6515.6	$F_{10,523} = 45.2$***	3090.2	$F_{12,523} = 31.05$***		
Hatch rate for 5 days oviposition	1375.2	$F_{10,523} = 26.2$***	919.5	$F_{12,523} = 11.0$***		
Juv. survival rate for 5 days oviposition	2035.3	$F_{10,523} = 26.3$***	1258.2	$F_{12,523} = 8.58$***		
Sex ratio for 5 days oviposition	517.0	$F_{10,523} = 8.69$***	538.4	$F_{12,523} = 8.69$***		
Oviposition period	408.2	$F_{10,523} = 26.3$***	123.3	$F_{12,707} = 15.5$***		
Adult longevity	394.2	$F_{20,707} = 57.3$***	94.88	$F_{12,707} = 12.6$***		
Total fecundity/female	14,707.5	$F_{20,707} = 33.1$***	22,430.1	$F_{12,707} = 38.4$***		
Net reproduction rate (R_0)	183.2	$F_{20,707} = 63.1$***	209.3	$F_{12,707} = 53.4$***		
Intrinsic rate of increase (r_m)	9.20	$F_{20,707} = 61.5$***	2.35	$F_{12,707} = 28.8$***		

Table 2 continued

Response variable	Full model excl. temperature[c]		Full model excl. species[d]		Full model excl. gender[e]	
	Deviance	Effect of temperature	Deviance	Effect of species	Deviance	Effect of gender
Mean generation time (t_G)	108,087.1	$F_{20,707} = 67.7$***	8389.4	$F_{12,707} = 27.2$***		

F-tests are based on Eq. 4

ns $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

[a] Deviance (*D*) is a measure of model quality. The null model is the model without any predictor variables. The lower the deviance of a given model relative to the deviance of the null model is, the better the fit

[b] The full model includes all predictor variables, i.e., species, temperature, temperature^2 and gender (only for egg-to-adult development) and their interactions. The *F*-test measures whether the full model is significantly better than the null model

[c] The *F*-test measures whether the increase in deviance by omitting all temperature terms from the full model is significant, i.e., temperature has an effect on the response variable

[d] The *F*-test measures whether the increase in deviance by omitting species from the full model is significant, i.e., the species differ with respect to the response variable

[e] The *F*-test measures whether the increase in deviance by omitting gender from the full model is significant, i.e., the genders differ with respect to response variable

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

Table 3 Temperature response of five *Tetranychus* species. *N* is the number of observations

Response variable	Species	*N*	Linear predictor function[a]
Egg-to-adult development[c]	***T. ludeni***		
	Female	387	$y = \mathbf{6.8406}(0.0910) - \mathbf{0.2902}(0.0076)T + \mathbf{0.0042}(0.0002)T^2$
	Male	287	$y = \mathbf{6.5827}(0.0842) - \mathbf{0.2697}(0.0070)T + \mathbf{0.0037}(0.0001)T^2$
	T. phaselus		
	Female	372	$y = \mathbf{5.1017}(0.0610) - \mathbf{0.143}9(0.0048)T + \mathbf{0.0014}(0.0001)T^2$
	Male	215	$y = \mathbf{5.1439}(0.1093) - \mathbf{0.14382}(0.0085)T + \mathbf{0.0014}(0.0002)T^2$
	T. piercei		
	Female	298	$y = \mathbf{5.6059}(0.0815) - \mathbf{0.1865}(0.0065)T + \mathbf{0.0022}(0.0001)T^2$
	Male	215	$y = \mathbf{5.3564}(0.0911) - \mathbf{0.1680}(0.0071)T + \mathbf{0.0018}(0.0001)T^2$
	T. truncatus		
	Female	399	$y = \mathbf{5.8010}(0.0547) - \mathbf{0.2049}(0.0043)T + \mathbf{0.0024}(0.0001)T^2$
	Male	218	$y = \mathbf{5.6426}(0.0728) - \mathbf{0.1967}(0.0055)T + \mathbf{0.0023}(0.0001)T^2$
	T. urticae		
	Female	455	$y = \mathbf{6.1996}(0.0863) - \mathbf{0.2478}(0.0070)T + \mathbf{0.0034}(0.0001)T^2$
	Male	255	$y = \mathbf{6.7692}(0.1086) - \mathbf{0.2880}(0.0087)T + \mathbf{0.0041}(0.0002)T^2$
Eggs/female for 5 days oviposition[e]	***T. ludeni***	145	$y = -\mathbf{3.2017}(0.2196) + \mathbf{0.4954}(0.0170)T - \mathbf{0.0079}(0.0003)T^2$
	T. phaselus	69	$y = 0.6872(0.4089) + \mathbf{0.1617}(0.0325)T - \mathbf{0.0023}(0.0006)T^2$
	T. piercei	86	$y = -0.5779(0.3860) + \mathbf{0.2469}(0.0309)T - \mathbf{0.0036}(0.0006)T^2$
	T. truncatus	96	$y = \mathbf{1.4332}(0.2778) + \mathbf{0.1147}(0.0225)T - \mathbf{0.0011}(0.0004)T^2$
	T. urticae	156	$y = -\mathbf{3.0544}(0.2561) + \mathbf{0.4653}(0.0206)T - \mathbf{0.0078}(0.0004)T^2$
Hatch rate for 5 days oviposition[d]	***T. ludeni***	145	$y = 0.5388(2.2877) + \mathbf{0.4326}(0.1638)T - \mathbf{0.0116}(0.0029)T^2$
	T. phaselus	69	$y = 1.1464(1.9734) + 0.1506(0.1639)T - 0.0021(0.0032)T^2$
	T. piercei	72	$y = 0.5645(1.8174) + \mathbf{0.2886}(0.1461)T - \mathbf{0.0064}(0.0028)T^2$
	T. truncatus	96	$y = 1.8429(2.8884) + 0.3206(0.2194)T - \mathbf{0.0086}(0.0040)T^2$
	T. urticae	156	$y = 0.1022(1.2375) + \mathbf{0.3389}(0.0976)T - \mathbf{0.0079}(0.0019)T^2$

Table 3 continued

Response variable	Species	N	Linear predictor function[a]
Juv. survival for 5 days oviposition[d]	***T. ludeni***	145	$y = -\mathbf{5.2202}(1.8449) + \mathbf{0.8432}(0.1415)T - \mathbf{0.0190}(0.0026)T^2$
	T. phaselus	69	$y = -2.9999(2.4381) + \mathbf{0.5650}(0.1992)T - \mathbf{0.0117}(0.0038)T^2$
	T. piercei	72	$y = 1.0381(2.1869) + 0.2415(0.1701)T - 0.0061(0.0032)T^2$
	T. truncatus	96	$y = -0.7995(0.5505) + \mathbf{0.1814}(0.0450)T - \mathbf{0.0039}(0.0009)T^2$
	T. urticae	156	$y = 0.8842(1.3552) + 0.1962(0.1073)T - \mathbf{0.0049}(0.0021)T^2$
Sex ratio for 5 days oviposition[d]	***T. ludeni***	145	$y = -\mathbf{1.9966}(0.5416) + \mathbf{0.2443}(0.0440)T - \mathbf{0.0042}(0.0009)T^2$
	T. phaselus	69	$y = 1.6921(0.9874) - 0.0429(0.0786)T + 0.0009(0.0015)T^2$
	T. piercei	72	$y = 1.2036(0.6446) - 0.0018(0.0528)T + 0.0002(0.0010)T^2$
	T. truncatus	96	$y = \mathbf{1.8320}(0.5604) - 0.0339(0.0455)T + 0.0006(0.0009)T^2$
	T. urticae	156	$y = -\mathbf{0.7995}(0.5505) + 0.1814(0.0450)T - 0.0039(0.0009)T^2$
Oviposition period[c]	***T. ludeni***	180	$y = \mathbf{5.7114}(0.2953) - \mathbf{0.1624}(0.0253)T + \mathbf{0.0015}(0.0005)T^2$
	T. phaselus	125	$y = -0.1549(0.6340) + \mathbf{0.3417}(0.0519)T - \mathbf{0.0089}(0.0010)T^2$
	T. piercei	103	$y = \mathbf{2.7887}(0.6189) + 0.0238(0.0510)T - 0.0016(0.0010)T^2$
	T. truncatus	143	$y = \mathbf{2.7658}(0.4439) + 0.0608(0.0371)T - \mathbf{0.0028}(0.0007)T^2$
	T. urticae	171	$y = \mathbf{2.8214}(0.4090) + \mathbf{0.0839}(0.0351)T - \mathbf{0.0037}(0.0007)T^2$
Adult longevity[c]	***T. ludeni***	180	$y = \mathbf{6.2211}(0.2922) - \mathbf{0.1956}(0.0250)T + \mathbf{0.0022}(0.0005)T^2$
	T. phaselus	125	$y = \mathbf{1.5498}(0.5274) + \mathbf{0.2234}(0.0432)T - \mathbf{0.0064}(0.0008)T^2$
	T. piercei	103	$y = \mathbf{4.0206}(0.4957) - 0.0451(0.0408)T - 0.0003(0.0008)T^2$
	T. truncatus	143	$y = \mathbf{3.3893}(0.3841) + 0.0447(0.0321)T - \mathbf{0.0027}(0.0006)T^2$
	T. urticae	171	$y = \mathbf{3.3794}(0.4108) + 0.0657(0.0353)T - \mathbf{0.0035}(0.0007)T^2$
Total oviposition/female[e]	***T. ludeni***	180	$y = \mathbf{4.0723}(0.2970) + \mathbf{0.142}(0.0262)T - \mathbf{0.0033}(0.0005)T^2$
	T. phaselus	125	$y = -\mathbf{1.9265}(0.7460) + \mathbf{0.5164}(0.0609)T - \mathbf{0.0109}(0.0012)T^2$
	T. piercei	103	$y = 1.1239(1.1854) + \mathbf{0.2152}(0.0962)T - \mathbf{0.0041}(0.0019)T^2$
	T. truncatus	143	$y = \mathbf{2.1803}(0.4924) + \mathbf{0.2105}(0.0412)T - \mathbf{0.0046}(0.0008)T^2$
	T. urticae	171	$y = -\mathbf{1.6331}(0.4551) + \mathbf{0.5649}(0.0388)T - \mathbf{0.0124}(0.0008)T^2$

Table 3 continued

Response variable	Species	N	Linear predictor function[a]
Net reproductive rate (R_0)[c]	***T. ludeni***	180	$y = \mathbf{2.5122}(0.0421) + \mathbf{0.2395}(0.0036)T - \mathbf{0.0058}(0.0001)T^2$
	T. phaselus	125	$y = \mathbf{-2.4891}(0.2600) + \mathbf{0.5447}(0.0213)T - \mathbf{0.0116}(0.0004)T^2$
	T. piercei	103	$y = \mathbf{1.0523}(0.4848) + \mathbf{0.1979}(0.0399)T - \mathbf{0.0039}(0.0008)T^2$
	T. truncatus	143	$y = \mathbf{1.4479}(0.2103) + \mathbf{0.2624}(0.0176)T - \mathbf{0.0060}(0.0003)T^2$
	T. urticae	171	$y = \mathbf{-2.1843}(0.5057) + \mathbf{0.6211}(0.0445)T - \mathbf{0.0137}(0.0001)T^2$
Intrinsic rate of increase (r_m)[b]	***T. ludeni***	180	$y = \mathbf{2.1955}(0.1023) - \mathbf{0.3148}(0.0134)T + \mathbf{0.0149}(0.0006)T^2 - \mathbf{0.000021}(0.00001)T^3$
	T. phaselus	125	$y = \mathbf{1.3395}(0.2664) - \mathbf{0.1887}(0.0341)T + \mathbf{0.0089}(0.0014)T^2 - \mathbf{0.00013}(0.00002)T^3$
	T. piercei	103	$y = \mathbf{1.5961}(0.2082) - \mathbf{0.2228}(0.0268)T + \mathbf{0.0103}(0.0011)T^2 - \mathbf{0.00014}(0.00001)T^3$
	T. truncatus	143	$y = 0.2156(0.1172) - \mathbf{0.0300}(0.0152)T + 0.0019(0.0006)T^2 - \mathbf{0.00003}(0.00001)T^3$
	T. urticae	171	$y = -0.0803(0.1257) - 0.0147(0.0166)T + \mathbf{0.0024}(0.0007)T^2 - \mathbf{0.00005}(0.00001)T^3$
Mean generation time (t_G)[c]	***T. ludeni***	180	$y = \mathbf{6.9006}(0.1217) - \mathbf{0.2568}(0.0104)T + \mathbf{0.0036}(0.0002)T^2$
	T. phaselus	125	$y = \mathbf{4.8435}(0.2733) - \mathbf{0.0811}(0.0224)T + 0.0001(0.0004)T^2$
	T. piercei	103	$y = \mathbf{5.6926}(0.2170) - \mathbf{0.1631}(0.0179)T + \mathbf{0.0018}(0.0003)T^2$
	T. truncatus	143	$y = \mathbf{4.9399}(0.0980) - \mathbf{0.0974}(0.0082)T + \mathbf{0.0004}(0.0002)T^2$
	T. urticae	171	$y = \mathbf{7.0771}(0.1127) - \mathbf{0.2697}(0.0097)T + \mathbf{0.0037}(0.0002)T^2$

Significant ($P < 0.05$) parameter values are shown in bold. Species shown in bold exhibit a significant response ($P < 0.05$) to temperature (T)

[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] The dependent variable y is normally distributed. The link function is identity

[c] The dependent variable y is log-transformed and assumed to be normally distributed. The link function is identity. Back-transformed values are obtained as $y^* = e^y$

[d] The dependent variable y binomially distributed. The link function is logit. Back-transformed values are obtained as $y^* = e^y/(1 + e^y)$

[e] The dependent variable y is Poisson distributed. The link function is logarithmic. Back-transformed values are obtained as $y^* = e^y$

variance, to make the residuals more normally distributed, and to ensure that the back-transformed values were non-negative.

To test for differences in temperature responses among species and between genders, we compared the deviance of the full model with the increase in deviance resulting from omitting species and gender from the full model, whereas the overall effect of temperature was tested by omitting this factor from the full model. The difference between the full model and a reduced model (i.e., a model with fewer factors) was tested by means of Manly's (1990) test:

$$F_{v_1,v_2} = \frac{(D_1 - D_2)/(p_2 - p_1)}{D_2/(N - p_2 - 1)} \tag{4}$$

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 for F are given as $v_1 = p_2 - p_1$ and $v_2 = N - p_2 - 1$. Large values of F indicate that the factor(s) omitted from the full model contributed significantly ($P < 0.05$) to explain variation in the dependent variable (y).

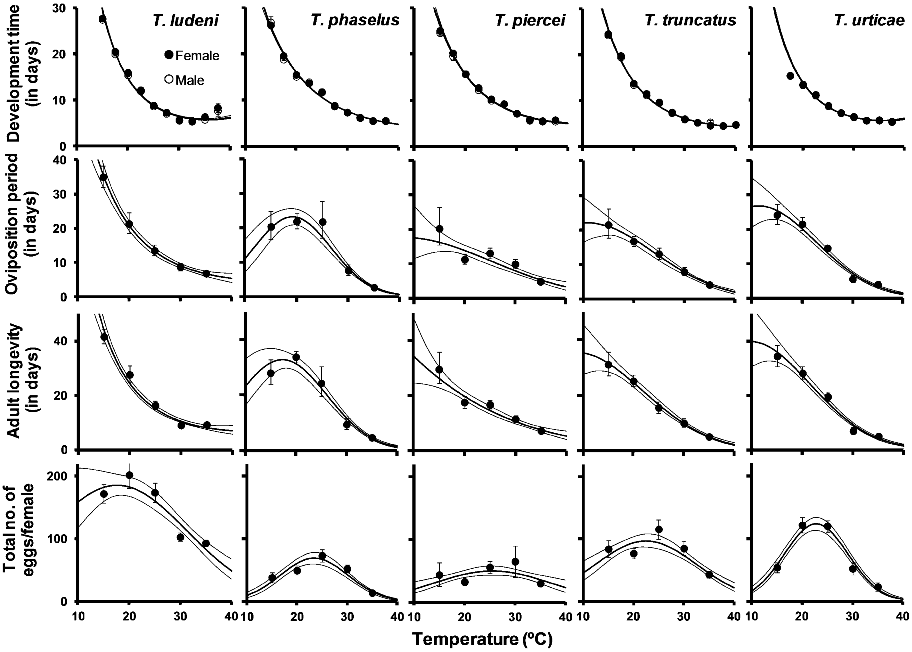

Fig. 1 Effect of temperature on developmental time from egg to adult, mean duration of the oviposition period, adult longevity and total fecundity in the five *Tetranychus* species kept on common bean at various temperatures and a 16L:8D photoperiod. See Appendixes 1 and 2 for further information. Points 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 3

Results

Immature development

No eggs of *T. ludeni* (0/96) and *T. urticae* (0/96) hatched at 40 °C, whereas most of the hatched individuals did not reach to the adult stage in the other three species (Appendix 1).

Table 4 Estimated values of constants in linear and non-linear models describing the relationship between temperature (°C) and developmental rates of five *Tetranychus* species on bean leaf discs[a]

Stage and species	Law of total effective temperature linear model (Ikemoto and Takai's method)				Thermodynamic non-linear model		
	t (±SE)	*k* (±SE)	Linear model equation	r^2	T_Φ	95 % CI	χ^2
Egg-to-female adult							
T. ludeni	11.34 ± 0.70	123.71 ± 10.64	$y = 0.0081x - 0.0917$	0.9771	24.18	23.67–24.23	0.0023
T. phaselus	9.91 ± 0.77	153.60 ± 10.62	$y = 0.0065x - 0.0645$	0.9744	18.04	17.72–28.65	0.0012
T. piercei	9.81 ± 0.67	152.53 ± 9.50	$y = 0.0066x - 0.0643$	0.9771	26.54	25.66–27.04	0.0012
T. truncatus	10.88 ± 0.63	123.30 ± 8.02	$y = 0.0081x - 0.0883$	0.9753	27.41	26.69–27.88	0.0013
T. urticae	11.22 ± 0.46	118.31 ± 6.85	$y = 0.0085x - 0.0948$	0.9878	19.74	19.29–21.33	0.0040
Egg-to-male adult							
T. ludeni	11.30 ± 0.62	118.56 ± 9.17	$y = 0.0084x - 0.0953$	0.9713	24.36	24.32–25.39	0.0006
T. phaselus	9.90 ± 0.72	151.78 ± 9.82	$y = 0.0066x - 0.0652$	0.9741	28.22	27.92–29.85	0.0016
T. piercei	9.81 ± 0.66	147.40 ± 8.64	$y = 0.0068x - 0.0666$	0.9713	27.79	26.72–28.08	0.0017
T. truncatus	10.43 ± 0.51	127.24 ± 6.30	$y = 0.0079x - 0.0820$	0.9834	24.58	23.92–24.68	0.0028
T. urticae	11.66 ± 0.40	112.32 ± 6.31	$y = 0.0089x - 0.1038$	0.9904	20.56	19.87–20.63	0.0041
Egg-to-egg[b]							
T. ludeni	11.35 ± 0.71	137.29 ± 12.01	$y = 0.0073x - 0.0827$	0.9723	23.86	23.14–25.56	0.0024
T. phaselus	9.95 ± 0.77	170.42 ± 11.83	$y = 0.0059x - 0.0584$	0.9729	27.22	26.69–27.73	0.0014
T. piercei	9.81 ± 0.78	170.12 ± 12.34	$y = 0.0059x - 0.0578$	0.9723	25.16	24.01–25.35	0.0017
T. truncatus	10.61 ± 0.58	141.77 ± 8.14	$y = 0.0071x - 0.0748$	0.9778	27.18	26.72–28.12	0.0008
T. urticae	11.33 ± 0.46	130.66 ± 7.88	$y = 0.0077x - 0.0867$	0.9868	20.37	19.60–21.04	0.0040

[a] *t* lower thermal threshold (°C), *k* thermal constant (DD), $y = 1/D$, $x = 1/T$, *D* developmental time (days), *T* temperature (°C), T_Φ intrinsic optimum temperature (°C) and 95 % confidence interval (CI)

[b] Egg-to-egg is the time it takes for a female to develop from an egg to the moment she starts producing eggs herself

Table 5 Age in days for various reproductive parameters and peak oviposition rate in five *Tetranychus* species at various temperatures under a 16L:8D photoperiod

Temperature (°C)	Species	No. of females tested	First oviposition	Peak oviposition (oviposition rate)	First death occurred	All females died
15.0	*T. ludeni*	38	30	47 (7.4)	57	88
	T. phaselus	15	28	32 (3.5)	46	72
	T. piercei	14	28	31 (3.4)	44	74
	T. truncatus	24	26	34 (5.6)	43	77
	T. urticae	36	35	49 (2.6)	52	97
20.0	*T. ludeni*	30	18	28 (10.9)	33	62
	T. phaselus	39	17	24 (3.8)	37	67
	T. piercei	34	17	22 (3.6)	27	47
	T. truncatus	40	15	21 (7.5)	27	58
	T. urticae	40	14	22 (8.1)	32	56
25.0	*T. ludeni*	40	10	17 (17.9)	20	40
	T. phaselus	14	14	16 (7.7)	25	50
	T. piercei	14	11	15 (7.6)	23	31
	T. truncatus	13	11	15 (11.1)	22	31
	T. urticae	46	10	13 (13.4)	22	45
30.0	*T. ludeni*	45	7	10 (20.4)	12	22
	T. phaselus	22	8	10 (10.9)	13	27
	T. piercei	17	8	9 (9.7)	16	23
	T. truncatus	23	8	10 (14.5)	15	27
	T. urticae	31	7	9 (12.5)	11	25
35.0	*T. ludeni*	27	7	11 (18.9)	13	22
	T. phaselus	35	7	8 (4.9)	9	20
	T. piercei	24	6	9 (8.1)	11	18
	T. truncatus	43	6	7 (15.6)	8	15
	T. urticae	18	6	9 (6.5)	9	19

In *T. ludeni*, survival rate was also very low at 37.5 °C (10.5 %, $n = 67$). Immature survivorship (egg to adult) for the five *Tetranychus* species was similar between 15 and 35 °C ranging from 61.6 to 100 % (Appendix 1). Temperature strongly affected the egg-to-adult duration, and there was a significant difference between the five species with respect to how they responded to temperature (Tables 2, 3; Fig. 1). There was also a significant difference between genders with respect to developmental time in all species (Table 2). From 15 to 32.5 °C, the egg-to-adult developmental time of both sexes decreased with increasing temperature, whereas it became slightly longer at higher temperatures, especially in *T. ludeni* and *T. urticae* (Fig. 1; Appendix 1).

The linear model of Ikemoto and Takai (2000), when fitted to values of developmental rates, gave a close fit to the data in the temperature range between 15 and 30 °C ($0.9723 \leq r^2 \leq 0.9904$) (Table 4). The estimated lower thermal thresholds (t) for egg-to-adult and for egg-to-egg development were similar and the values ranged from 9.81 to 11.66 and from 9.81 to 11.35 °C, respectively, for the five *Tetranychus* species (Table 4). The thermal constant (k) for the respective stages ranged from 118.3 to 153.6 DD and from

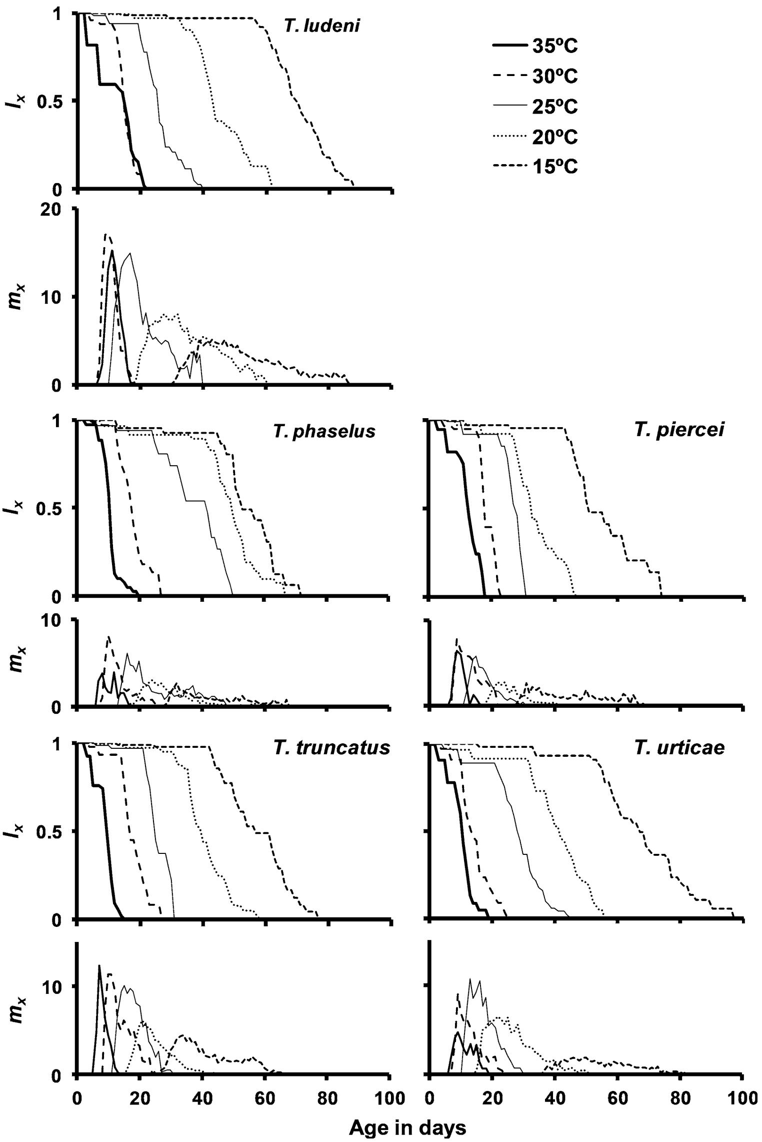

Fig. 2 Age-specific survival rate (l_x) and age-specific fecundity rate (m_x) of females of five *Tetranychus* species at five constant temperatures

130.7 to 170.4 DD, respectively (Table 4). The non-linear OptimSSI-P model, when fitted to values of developmental rates, gave a close fit to the data in the temperature range between 15 and 37.5 °C ($0.0008 \leq \chi^2 \leq 0.0041$) (Table 4). The intrinsic optimum temperature (T_Φ) ranged from 18.0 to 27.4 °C for egg-to-female adult, from 20.6 to 28.2 °C for egg-to-male adult and from 23.9 to 27.2 °C for egg-to-egg development (Table 4).

Reproduction

The pre-oviposition period decreased with increasing temperature from 15 to 35 °C for *T. truncatus* or to 30 °C for the other four species (Appendix 1). The oviposition period and adult longevity were also strongly affected by temperature (Appendix 2; Fig. 1). Total fecundity (eggs/female) was highest in *T. ludeni* at all five temperatures and lowest in *T. phaselus* at 15 and 35 °C, in *T. piercei* at 20 °C and in *T. urticae* at 30 °C (Fig. 1; Appendix 2). The difference between species with respect to total fecundity was highly significant (Table 2). For instance, at 20 °C total fecundity ranged from 32.2 eggs in *T. piercei* to 202.0 eggs in *T. ludeni* (Appendix 2).

The number of eggs laid during the first 5 days of the oviposition period, their hatchability, the survival rate of the immature stages and the proportion of female offspring are given in Appendix 3. The effect of temperature on these variables was also highly significant ($P < 0.001$) (Table 2).

Demographic parameters

The age-specific survival rate (l_x) started to drop at younger ages as the temperature increased from 15 to 35 °C (Table 5; Fig. 2). The age-specific fecundity rate (m_x) peaked at an earlier age and the oviposition period became shorter as the temperature increased. The peak oviposition rate was highest in *T. ludeni* at all five temperatures (Table 5). The age of the first oviposition decreased with increasing temperature for all five species.

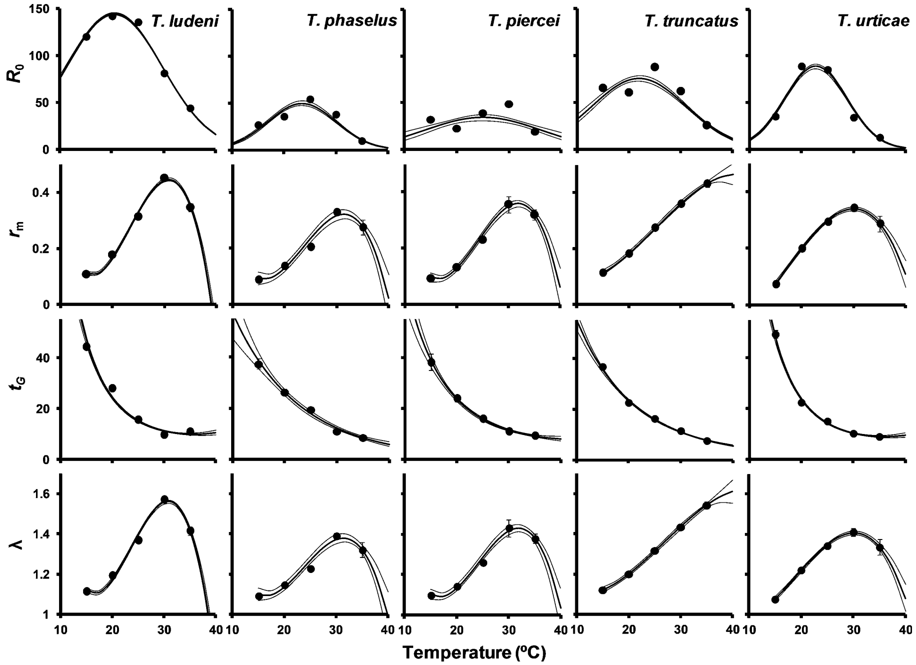

Fig. 3 Effect of temperature on demographic parameters of five *Tetranychus* species. See Appendix 4 for further information. R_0, net reproductive rate; r_m, intrinsic rate of natural increase; t_G, mean generation time; λ, finite rate of increase. Points show the sample averages with 95 % confidence 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 3

The net reproductive rate (R_0), the intrinsic rate of natural increase (r_m, day^{-1}), the mean generation time (t_G, days) and doubling time (t_D, days) were all affected by temperature and there were significant differences among the five species with respect to temperature response (Tables 2, 3; Fig. 3; Appendix 4). The highest R_0 value was observed in *T. ludeni* at all five temperatures (Appendix 4). The species with the highest r_m value varied with temperature: *T. truncatus* at 15 °C (0.1141 day^{-1}) and at 35 °C (0.4330 day^{-1}), *T. urticae* at 20 °C (0.1998 day^{-1}), and *T. ludeni* at 25 °C (0.3138 day^{-1}) and 30 °C (0.4514 day^{-1}) (Appendix 4). The values of r_m and λ increased with increasing temperature from 15 to 30 or 35 °C in all five species. Mean generation time (t_G) and doubling time (t_D) decreased with increasing temperature (Fig. 3; Appendix 4).

Discussion

The present study shows that total fecundity, R_0 and r_m of *T. ludeni* were higher than those of *T. urticae* at all five temperatures tested. It indicates that *T. ludeni* has a high potential to become a serious pest. *T. piercei* and *T. truncatus* showed higher r_m-values at 30 and 35 °C than that of *T. urticae*, suggesting that these two species as well as *T. ludeni* are better adapted to hot weather than *T. urticae* (Appendix 4). The lower thermal thresholds in the five *Tetranychus* species were in the order *T. urticae* $\approx$ *T. ludeni* $>$ *T. truncatus* $>$ *T. phaselus* $\approx$ *T. piercei* (Table 4). T_Φ, which is the most important parameter for development because it exhibits the minimum effects on enzyme inactivation related to development at low and high temperature (Ikemoto 2008), was higher in the four minor species than in *T. urticae*. Development and reproduction of arthropods are considered to be gradually inhibited at temperatures far from T_Φ. As the ambient temperatures are expected to increase dramatically during the coming years due to global warming (Chen et al. 2013; Kiritani 2013; Estay et al. 2014), the species having a high T_Φ are likely to increase their abundance in temperate regions and eventually replace *T. urticae* as major pests. Accordingly, *T. ludeni*, *T. piercei* and *T. truncatus* have the potential to become serious pests. Consequently, if the use of agrochemicals is restricted, we can expect that the invasion of these until now minor species into crop fields will be accelerated.

The thermal threshold (t) of development from egg to adult female has been found to range from 7.8 to 13.8 °C in the genus *Tetranychus*. In our study, thermal thresholds ranged from 9.8 to 11.7 °C (Table 4), which fall within the previously reported range. The thermal threshold of *T. truncatus* from Japan was found to be 10.9 °C, which is lower than the one found for the same species in Thailand (11.6 °C; Sakunwarin et al. 2003) and China (13.9 °C; Fan et al. 2003). The thermal threshold of *T. urticae* in this study (11.2 °C) was in-between the one obtained from an Australian population (7.8 °C; Davies et al. 2009) and the one from an Iranian population (13.8 °C; Riahi et al. 2013). Thus, the threshold values vary greatly among populations and probably reflect adaptations to the local climate.

The intrinsic rate of natural increase (r_m) calculated by other authors for *Tetranychus* species are difficult to compare with our results, as differences could be due to the local strains used as well as to differences in experimental methodology, for instance with respect to the size and type of experimental arenas, host plants used, relative humidity, photoperiod and differences in calculation methods (Bonato 1999; Ferrero et al. 2007). Nevertheless, Sabelis (1985, 1991), in an extensive review of life-history parameters of tetranychid mites, found r_m-values for *Tetranychus* mites to range from 0.200 to 0.336 day^{-1} at ca. 25 °C. The r_m-values of the five *Tetranychus* species in this study fall within this range. The r_m-values of *T. truncatus* increased with increasing temperature form 15 °C (0.1141 day^{-1}) to 35 °C (0.4330 day^{-1}) in contrast to the decline observed in *Tetranychus merganser* Boudreaux at the highest temperature (Ullah et al. 2011). The r_m-value (0.275 day^{-1}) and R_0-value (88.0) of the Japanese *T. truncatus* are noticeably higher than those of the Thai population, which were found as 0.173 day^{-1} and 37.39, respectively (Sakunwarin et al. 2003). This discrepancy could be attributed to differences in developmental time (12.5 vs 10.1 days; Thai vs Japanese population), peak oviposition (6.5 vs 11.1 eggs on day 15 for both), and total fecundity (65.6 vs 115.9 eggs). The r_m-value (0.193 day^{-1}) and R_0-value (21.7) of the Chinese strain of *T. truncatus* on common bean (Pang et al. 2004) are much lower than those of the Japanese strain in spite of the fact that the former was examined at 28 °C. The developmental time (9.4 days for female) of the Chinese *T. truncatus* strain is longer than the one found in our study at 27.5 °C (7.6 days). The reason for this difference is not clear because the peak oviposition age and oviposition rates were not reported by Pang et al. (2004). In general, the two parameters of paramount importance in determining the r_m-value are developmental time and the peak oviposition rate (Snell 1978; Wrensch 1985).

The r_m-value (0.294 day^{-1} at 25 °C) of *T. urticae* in our study is comparable to the value (0.292 day^{-1}) reported by Kondo and Takafuji (1985) and the value (0.259 day^{-1}) by Saito (1979), which are much higher than the r_m-values reported by some other authors (0.144–0.188 day^{-1}) (Bounfour and Tanigoshi 2001; Khanamani et al. 2013; Riahi et al. 2013). In all of the latter reports, the R_0-values are also much lower than the one found in our study. The r_m-value of *T. ludeni* (0.314 day^{-1}) is comparable to that of *T. okinawanus* (0.316 day^{-1}) at 25 °C (Takafuji et al. 1996), which is the second highest value reported for a *Tetranychus* species so far. The reproductive traits of *T. ludeni* are similar to or higher than those of other pest mite species such as *T. urticae*, suggesting that *T. ludeni*, together with *T. piercei* and *T. truncatus*, have the potential to become serious pests.

In the present study, the five species were kept under the same laboratory conditions from 1 to 15 years prior to the experiments. We cannot preclude the possibility that the species have adapted to the laboratory conditions which might have affected their life-history characteristics. In fact, *Tetranychus pacificus* McGregor populations originating from various grapevine cultivars showed significant differences with respect to developmental time and juvenile survival, but no difference with respect to reproductive rate, when reared on a common host plant under the same laboratory conditions (Scranton et al. 2013). *Tetranychus urticae* has shown rapid adaptation to unfavourable host plants after 15 generations, causing an increase in juvenile survival and female fecundity but no variation in developmental time (Magalhaes et al. 2007). Therefore, further studies are required to clarify the effect of adaptation when laboratory populations have been subjected to the long-term exposure to laboratory conditions, for instance by comparing individuals from newly established cultures with individuals originating from populations reared under laboratory conditions for many years. In addition, research is needed to investigate the preference of natural enemies for feeding on the focal mite species and how agrochemicals influence their survival, development and reproduction in order to assess the risk of transforming these minor pests into major ones.

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Appendix 1

See Table 6.

Table 6 Developmental time (mean ± SE, days) from egg to adult, preoviposition period (mean ± SE, days) and percentage (%) of immature survival (egg to adult) of five *Tetranychus* species on bean leaf discs at various temperatures under a 16L:8D photoperiod

Temperature and item		Species									
		N[a]	*T. ludeni*	*N*	*T. phaselus*	*N*	*T. piercei*	*N*	*T. truncatus*	*N*	*T. urticae* (G)
15.0	Egg-to-adult (♀)	38	28.0 ± 0.16	15	25.8 ± 0.22	14	25.6 ± 0.33	24	24.8 ± 0.15	36	32.6 ± 0.30
	Egg-to-adult (♂)	26	27.5 ± 0.19	11	26.8 ± 0.66	13	24.6 ± 0.21	12	24.3 ± 0.26	24	35.2 ± 0.70
	Pre-oviposition		2.9 ± 0.10		2.9 ± 0.17		1.8 ± 0.16		2.8 ± 0.11		4.5 ± 0.12
	Egg-to-egg		31.0 ± 0.19		28.7 ± 0.21		27.4 ± 0.31		27.5 ± 0.17		37.2 ± 0.33
	Immature survival[b]		97.0 [66][c]		86.7 [30]		81.8 [33]		90.0 [40]		89.6 [67]
17.5	Egg-to-adult (♀)	41	21.2 ± 0.13	44	19.8 ± 0.15	48	20.5 ± 0.19	47	19.9 ± 0.10	67	15.2 ± 0.07
	Egg-to-adult (♂)	46	20.0 ± 0.15	11	18.8 ± 0.12	10	19.6 ± 0.43	12	19.5 ± 0.31	22	15.3 ± 0.17
	Pre-oviposition		2.7 ± 0.10		2.0 ± 0.04		2.6 ± 0.11		1.8 ± 0.06		1.6 ± 0.07
	Egg-to-egg		23.9 ± 0.17		21.8 ± 0.15		23.1 ± 0.21		21.7 ± 0.11		16.8 ± 0.09
	Immature survival		94.6 [92]		89.7 [60]		91.6 [60]		98.3 [60]		97.8 [91]
20.0	Egg-to-adult (♀)	30	16.6 ± 0.11	39	15.9 ± 0.20	34	15.9 ± 0.13	40	14.2 ± 0.15	40	13.2 ± 0.10
	Egg-to-adult (♂)	28	15.4 ± 0.13	31	15.1 ± 0.16	37	15.7 ± 0.15	34	13.5 ± 0.14	29	13.4 ± 0.12
	Pre-oviposition		1.8 ± 0.10		2.9 ± 0.15		2.0 ± 0.09		1.9 ± 0.08		1.8 ± 0.08
	Egg-to-egg		18.4 ± 0.11		18.8 ± 0.28		17.9 ± 0.15		16.0 ± 0.15		15.0 ± 0.14
	Immature survival		85.3 [68]		94.6 [74]		94.7 [76]		94.9 [78]		95.8 [72]
22.5	Egg-to-adult (♀)	51	12.4 ± 0.08	43	13.6 ± 0.11	44	13.0 ± 0.14	47	11.7 ± 0.11	68	11.2 ± 0.06
	Egg-to-adult (♂)	43	12.0 ± 0.09	13	13.9 ± 0.18	15	12.3 ± 0.21	13	11.3 ± 0.18	24	11.0 ± 0.06
	Pre-oviposition		1.2 ± 0.07		1.2 ± 0.06		1.8 ± 0.09		1.3 ± 0.06		1.2 ± 0.05
	Egg-to-egg		13.7 ± 0.10		14.8 ± 0.14		14.8 ± 0.17		12.9 ± 0.12		12.4 ± 0.07
	Immature survival		97.9 [96]		92.9 [58]		95.7 [60]		100.0 [60]		97.9 [94]
25.0	Egg-to-adult (♀)	40	9.1 ± 0.07	14	12.0 ± 0.15	19	10.6 ± 0.11	17	10.1 ± 0.06	46	8.9 ± 0.07
	Egg-to-adult (♂)	31	8.7 ± 0.08	16	11.7 ± 0.25	18	10.0 ± 0.11	23	9.6 ± 0.11	25	8.7 ± 0.15
	Pre-oviposition		1.0 ± 0.06		1.1 ± 0.10		1.2 ± 0.10		1.0 ± 0.00		1.0 ± 0.05
	Egg-to-egg		10.1 ± 0.08		13.1 ± 0.14		11.8 ± 0.12		11.1 ± 0.06		9.9 ± 0.08

Table 6 continued

Temperature and item		Species									
		N^a	*T. ludeni*	*N*	*T. phaselus*	*N*	*T. piercei*	*N*	*T. truncatus*	*N*	*T. urticae* (G)
	Immature survival		92.2 [77]		80.3 [35]		86.8 [40]		93.0 [43]		98.6 [72]
27.5	Egg-to-adult (♀)	54	7.6 ± 0.04	55	9.0 ± 0.07	23	9.3 ± 0.08	44	7.6 ± 0.05	63	7.3 ± 0.05
	Egg-to-adult (♂)	31	7.1 ± 0.06	30	8.7 ± 0.09	14	9.3 ± 0.13	13	7.4 ± 0.08	29	7.2 ± 0.11
	Pre-oviposition		0.7 ± 0.03		0.7 ± 0.04		0.9 ± 0.06		0.9 ± 0.03		0.7 ± 0.04
	Egg-to-egg		8.3 ± 0.05		9.8 ± 0.06		10.2 ± 0.08		8.4 ± 0.05		8.0 ± 0.06
	Immature survival		91.4 [93]		96.6 [88]		78.6 [45]		95.0 [60]		95.8 [96]
30.0	Egg-to-adult (♀)	45	5.9 ± 0.05	22	7.4 ± 0.07	17	7.3 ± 0.11	23	6.2 ± 0.05	31	6.6 ± 0.09
	Egg-to-adult (♂)	25	5.6 ± 0.06	11	7.4 ± 0.15	16	7.2 ± 0.08	19	6.0 ± 0.00	32	6.3 ± 0.06
	Pre-oviposition		0.5 ± 0.02		0.5 ± 0.02		0.7 ± 0.06		0.8 ± 0.05		0.7 ± 0.04
	Egg-to-egg		6.4 ± 0.05		7.9 ± 0.08		8.0 ± 0.13		7.0 ± 0.02		7.3 ± 0.10
	Immature survival		89.7 [78]		82.5 [40]		82.5 [40]		93.3 [45]		86.3 [73]
32.5	Egg-to-adult (♀)	57	5.6 ± 0.04	58	6.4 ± 0.05	51	6.0 ± 0.05	66	5.4 ± 0.03	63	5.6 ± 0.03
	Egg-to-adult (♂)	27	5.4 ± 0.05	37	6.2 ± 0.07	25	5.7 ± 0.08	26	5.3 ± 0.07	21	5.6 ± 0.03
	Pre-oviposition		0.8 ± 0.03		0.5 ± 0.02		0.7 ± 0.04		0.8 ± 0.03		0.9 ± 0.03
	Egg-to-egg		6.5 ± 0.03		6.9 ± 0.05		6.7 ± 0.06		6.1 ± 0.04		6.5 ± 0.03
	Immature survival		91.3 [92]		100.0 [95]		91.6 [83]		96.8 [95]		89.4 [94]
35.0	Egg-to-adult (♀)	27	7.1 ± 0.14	35	5.5 ± 0.08	24	5.8 ± 0.09	43	4.5 ± 0.02	18	5.9 ± 0.13
	Egg-to-adult (♂)	27	5.8 ± 0.10	42	5.6 ± 0.09	39	5.5 ± 0.07	12	5.4 ± 0.21	27	5.6 ± 0.08
	Pre-oviposition		1.0 ± 0.08		0.9 ± 0.04		0.9 ± 0.05		0.7 ± 0.04		0.8 ± 0.09
	Egg-to-egg		8.1 ± 0.17		6.4 ± 0.07		6.7 ± 0.09		5.2 ± 0.05		6.7 ± 0.19
	Immature survival		69.2 [78]		84.6 [91]		80.8 [78]		88.7 [62]		61.6 [73]
37.5	Egg-to-adult (♀)	4	9.0 ± 0.29	47	5.5 ± 0.01	24	6.3 ± 0.09	37	4.7 ± 0.03	23	5.4 ± 0.11
	Egg-to-adult (♂)	3	7.7 ± 0.60	13	5.6 ± 0.06	28	5.5 ± 0.07	39	4.6 ± 0.04	22	5.3 ± 0.06
	Pre-oviposition		1.0 ± 0.00		0.9 ± 0.02		1.0 ± 0.05		0.7 ± 0.03		0.9 ± 0.06

Table 6 continued

Temperature and item		Species									
		N^a	*T. ludeni*	*N*	*T. phaselus*	*N*	*T. piercei*	*N*	*T. truncatus*	*N*	*T. urticae* (G)
	Egg-to-egg		10.0 ± 0.29		6.4 ± 0.02		7.2 ± 0.08		5.4 ± 0.03		6.4 ± 0.11
	Immature survival		10.5 [67]		65.2 [92]		57.1 [91]		82.6 [92]		50.0 [90]
40.0	Egg-to-adult (♀)		–	10	6.8 ± 0.18	3	7.1 ± 0.36	15	5.1 ± 0.17		–
	Egg-to-adult (♂)		–		–	1	6.5	15	4.7 ± 0.05		–
	Pre-oviposition		–		0.8 ± 0.05		0.8 ± 0.25		1.3 ± 0.14		–
	Egg-to-egg		–		7.5 ± 0.16		7.8 ± 0.42		6.3 ± 0.13		–
	Immature survival		0 [96]		15.6 [64]		5.1 [78]		32.6 [92]		0 [96]

[a] Number of individuals tested

[b] Percentage of development from egg to adult

[c] Number in brackets means number of eggs examined

Appendix 2

See Table 7.

Table 7 Duration (mean ± SE, days) of adult phases and oviposition rates (mean ± SE) in five *Tetranychus* species on bean leaf discs at five temperatures under a 16L:8D photoperiod

Temperature	Species	N^a	Oviposition	Post-oviposition	Longevity	Total eggs/female	Eggs/♀/day
15.0	*T. ludeni*	38	36.2 ± 1.45	3.3 ± 0.60	42.4 ± 1.36	171.9 ± 7.15	4.8 ± 0.14
	T. phaselus	15	21.5 ± 2.00	4.7 ± 0.46	29.1 ± 2.07	38.5 ± 3.64	1.9 ± 0.16
	T. piercei	14	22.4 ± 2.75	5.4 ± 0.46	31.1 ± 2.79	43.7 ± 8.77	1.9 ± 0.19
	T. truncatus	24	23.7 ± 2.00	6.2 ± 0.80	32.6 ± 2.03	84.3 ± 6.64	3.7 ± 0.14
	T. urticae	36	25.7 ± 1.55	6.2 ± 1.22	36.5 ± 2.08	54.2 ± 3.88	2.1 ± 0.07
20.0	*T. ludeni*	30	24.5 ± 1.51	2.4 ± 0.50	28.8 ± 1.54	202.0 ± 10.77	8.4 ± 0.21
	T. phaselus	39	22.8 ± 1.05	8.7 ± 0.98	34.5 ± 1.07	50.0 ± 3.55	2.2 ± 0.15
	T. piercei	34	12.2 ± 0.87	4.4 ± 0.62	18.6 ± 1.10	32.2 ± 2.98	2.6 ± 0.14
	T. truncatus	40	17.3 ± 0.72	6.8 ± 0.76	26.0 ± 1.07	77.2 ± 3.99	4.5 ± 0.15
	T. urticae	40	22.3 ± 0.98	5.0 ± 0.83	29.1 ± 1.11	121.6 ± 5.78	5.5 ± 0.17
25.0	*T. ludeni*	40	14.6 ± 0.83	1.5 ± 0.25	17.0 ± 0.85	173.9 ± 7.79	12.2 ± 0.22
	T. phaselus	14	23.4 ± 2.26	1.5 ± 0.37	25.9 ± 2.35	73.8 ± 4.49	3.6 ± 0.45
	T. piercei	14	13.4 ± 0.74	2.2 ± 0.44	16.9 ± 0.66	55.9 ± 4.66	4.2 ± 0.26
	T. truncatus	13	13.4 ± 0.83	1.5 ± 0.49	15.9 ± 0.92	115.9 ± 7.25	8.7 ± 0.37
	T. urticae	46	14.9 ± 0.50	4.5 ± 0.65	20.4 ± 0.86	120.1 ± 4.42	8.2 ± 0.26
30.0	*T. ludeni*	45	7.8 ± 0.24	0.9 ± 0.22	9.2 ± 0.35	102.7 ± 3.15	13.4 ± 0.31
	T. phaselus	22	8.4 ± 0.85	1.4 ± 0.33	10.3 ± 0.93	52.6 ± 3.08	7.3 ± 0.52
	T. piercei	17	10.4 ± 0.65	0.7 ± 0.19	11.7 ± 0.57	64.9 ± 11.82	6.6 ± 1.17
	T. truncatus	23	8.5 ± 0.69	1.3 ± 0.27	10.6 ± 0.78	85.2 ± 5.31	10.3 ± 0.33
	T. urticae	31	6.2 ± 0.55	1.1 ± 0.41	8.0 ± 0.73	52.2 ± 4.85	8.3 ± 0.39
35.0	*T. ludeni*	27	6.9 ± 0.23	1.6 ± 0.38	9.4 ± 0.43	93.2 ± 2.45	13.7 ± 0.35
	T. phaselus	35	3.0 ± 0.30	1.1 ± 0.22	5.0 ± 0.39	14.3 ± 1.96	4.6 ± 0.37
	T. piercei	24	5.3 ± 0.37	1.5 ± 0.42	7.7 ± 0.51	30.0 ± 2.55	5.7 ± 0.26
	T. truncatus	43	4.4 ± 0.22	0.3 ± 0.08	5.4 ± 0.25	43.3 ± 2.70	10.0 ± 0.39
	T. urticae	18	4.4 ± 0.60	0.2 ± 0.13	5.4 ± 0.56	23.2 ± 3.35	5.5 ± 0.48

[a] No. of females tested

Appendix 3

See Table 8.

Table 8 Number of eggs laid (mean ± SE) during the first 5 days of the oviposition period, hatchability of eggs, survival rate of immature stages and female percentage reaching adulthood in five *Tetranychus* species at five temperatures under a 16L:8D photoperiod

Temperature	Species	N[a]	No. of eggs laid	% hatch	% survival	% female
15.0	*T. ludeni*	36	13.28 ± 0.35	98.72 ± 0.49	98.04 ± 0.58	72.27 ± 1.12
	T. phaselus	11	13.91 ± 0.79	95.41 ± 1.11	96.82 ± 1.36	75.71 ± 2.51
	T. piercei	17	11.82 ± 0.44	96.74 ± 1.12	98.39 ± 0.89	77.87 ± 1.29
	T. truncatus	20	19.90 ± 0.67	99.06 ± 0.44	98.53 ± 0.62	79.90 ± 1.59
	T. urticae	45	8.84 ± 0.26	98.18 ± 0.60	95.23 ± 0.85	70.48 ± 1.25
20.0	*T. ludeni*	34	31.82 ± 0.91	99.21 ± 0.34	97.68 ± 0.46	72.55 ± 1.30
	T. phaselus	14	19.36 ± 1.24	96.38 ± 1.05	95.13 ± 1.19	78.37 ± 2.46
	T. piercei	12	13.50 ± 0.68	97.15 ± 1.03	94.87 ± 1.80	77.05 ± 2.21
	T. truncatus	25	22.88 ± 1.15	99.50 ± 0.38	97.94 ± 0.76	80.97 ± 1.33
	T. urticae	32	24.84 ± 0.71	96.85 ± 0.56	94.47 ± 0.73	80.39 ± 1.02
25.0	*T. ludeni*	34	31.82 ± 0.91	99.21 ± 0.34	97.68 ± 0.46	72.55 ± 1.30
	T. phaselus	13	26.23 ± 1.59	96.43 ± 0.89	97.27 ± 1.19	78.62 ± 2.32
	T. piercei	13	28.23 ± 2.22	98.80 ± 0.57	92.74 ± 1.31	76.78 ± 1.81
	T. truncatus	16	44.69 ± 2.47	98.74 ± 0.54	98.01 ± 0.47	78.44 ± 1.33
	T. urticae	35	36.37 ± 1.05	96.99 ± 0.39	91.99 ± 1.13	79.97 ± 1.10
30.0	*T. ludeni*	24	102.75 ± 1.85	95.84 ± 1.09	97.67 ± 0.53	84.52 ± 0.98
	T. phaselus	16	33.00 ± 1.31	98.67 ± 0.54	98.43 ± 0.58	74.63 ± 1.54
	T. piercei	17	39.12 ± 1.94	96.60 ± 0.73	97.89 ± 0.48	79.94 ± 1.21
	T. truncatus	20	46.55 ± 1.92	97.84 ± 0.69	95.47 ± 0.98	78.22 ± 1.19
	T. urticae	29	55.86 ± 2.19	97.11 ± 0.46	93.76 ± 1.18	72.50 ± 1.23
35.0	*T. ludeni*	27	79.15 ± 1.60	81.78 ± 1.30	72.31 ± 1.63	80.08 ± 1.30
	T. phaselus	15	33.20 ± 2.85	97.21 ± 0.63	90.97 ± 1.83	77.96 ± 2.61
	T. piercei	13	35.77 ± 2.89	94.53 ± 0.74	86.53 ± 1.72	79.63 ± 1.82
	T. truncatus	15	61.93 ± 2.70	92.59 ± 1.29	84.03 ± 1.72	79.45 ± 1.10
	T. urticae	15	36.93 ± 4.53	90.88 ± 0.94	85.35 ± 2.40	72.99 ± 2.68

[a] No. of individuals tested

Appendix 4

See Table 9.

Table 9 Demographic parameters (mean ± SE) of five *Tetranychus* species at five temperatures under a 16L:8D photoperiod

Temperature	Species	N^a	R_0	r_m	t_G	λ	t_D
15.0	*T. ludeni*	38	120.22 ± 0.14	0.1081 ± 0.0012	44.38 ± 0.33	1.1142 ± 0.0009	6.42 ± 0.05
	T. phaselus	15	26.95 ± 0.18	0.0883 ± 0.0019	37.58 ± 0.88	1.0923 ± 0.0021	7.91 ± 0.17
	T. piercei	14	32.40 ± 0.50	0.0922 ± 0.0033	38.38 ± 1.37	1.0966 ± 0.0038	7.64 ± 0.25
	T. truncatus	24	65.70 ± 0.23	0.1141 ± 0.0016	36.78 ± 0.42	1.1209 ± 0.0014	6.09 ± 0.07
	T. urticae (G)[b]	36	35.71 ± 0.07	0.0729 ± 0.0018	49.50 ± 0.79	1.0756 ± 0.0013	9.59 ± 0.15
20.0	*T. ludeni*	30	142.06 ± 0.26	0.1771 ± 0.0017	28.03 ± 0.20	1.1937 ± 0.0014	3.92 ± 0.03
	T. phaselus	39	35.91 ± 0.07	0.1371 ± 0.0050	26.63 ± 0.62	1.1472 ± 0.0036	5.15 ± 0.12
	T. piercei	34	22.89 ± 0.06	0.1318 ± 0.0045	24.17 ± 0.55	1.1410 ± 0.0035	5.35 ± 0.12
	T. truncatus	40	60.89 ± 0.08	0.1826 ± 0.0033	22.60 ± 0.23	1.2004 ± 0.0024	3.81 ± 0.04
	T. urticae	40	89.44 ± 0.11	0.1998 ± 0.0030	22.57 ± 0.22	1.2212 ± 0.0022	3.48 ± 0.03
25.0	*T. ludeni*	40	135.68 ± 0.16	0.3138 ± 0.0028	15.67 ± 0.09	1.3687 ± 0.0023	2.21 ± 0.01
	T. phaselus	14	54.41 ± 0.26	0.2051 ± 0.0038	19.57 ± 0.37	1.2278 ± 0.0049	3.40 ± 0.06
	T. piercei	14	39.30 ± 0.25	0.2301 ± 0.0046	16.05 ± 0.35	1.2589 ± 0.0061	3.03 ± 0.06
	T. truncatus	13	88.00 ± 0.46	0.2754 ± 0.0027	16.28 ± 0.20	1.3171 ± 0.0038	2.52 ± 0.03
	T. urticae	46	85.69 ± 0.07	0.2943 ± 0.0042	15.17 ± 0.13	1.3423 ± 0.0032	2.36 ± 0.02
30.0	*T. ludeni*	45	81.26 ± 0.06	0.4514 ± 0.0059	9.77 ± 0.07	1.5709 ± 0.0053	1.54 ± 0.01
	T. phaselus	22	38.11 ± 0.11	0.3290 ± 0.0070	11.14 ± 0.20	1.3901 ± 0.0081	2.12 ± 0.04
	T. piercei	17	49.04 ± 0.56	0.3565 ± 0.0147	11.19 ± 0.44	1.4305 ± 0.0199	1.99 ± 0.07
	T. truncatus	23	62.27 ± 0.18	0.3608 ± 0.0033	11.47 ± 0.09	1.4346 ± 0.0038	1.92 ± 0.01
	T. urticae	31	34.48 ± 0.11	0.3436 ± 0.0091	10.42 ± 0.20	1.4109 ± 0.0089	2.04 ± 0.04
35.0	*T. ludeni*	27	44.11 ± 0.05	0.3469 ± 0.0091	11.01 ± 0.19	1.4155 ± 0.0099	2.02 ± 0.04
	T. phaselus	35	9.85 ± 0.04	0.2749 ± 0.0201	8.93 ± 0.39	1.3203 ± 0.0180	2.70 ± 0.11
	T. piercei	24	19.54 ± 0.07	0.3192 ± 0.0104	9.46 ± 0.25	1.3770 ± 0.0114	2.21 ± 0.06
	T. truncatus	43	25.85 ± 0.04	0.4330 ± 0.0095	7.56 ± 0.10	1.5429 ± 0.0087	1.61 ± 0.02
	T. urticae	18	13.15 ± 0.11	0.2876 ± 0.0143	9.21 ± 0.34	1.3352 ± 0.0184	2.48 ± 0.09

[a] Number of females tested

[b] Green form

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