



Temperature-dependent development and reproduction of *Tarsonemus confusus* (Acari: Tarsonemidae): an important pest mite of horticulture

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Abstract

The tarsonemid mite *Tarsonemus confusus* Ewing has become an economically important pest in orchards in China. This study investigated the temperature-dependent development and reproduction of *T. confusus* at 15, 20, 25, 30, 33 and 35 °C. Eggs failed to hatch at 35 °C. When temperature increased from 15 to 30 °C, the developmental rate of eggs, larvae and quiescent larvae and that from egg to adulthood of both sexes significantly increased, and the time period required by females to commence oviposition significantly decreased. The lower temperature threshold (T_0) for the development of eggs, larvae and quiescent larvae was between 9.3 and 12.0 °C and both sexes required about 60 degree days (DD) to complete a life cycle. Females were expected to start oviposition at 12.9 °C. The number of eggs laid, the number of female offspring produced and the egg hatch rate were significantly higher at 20, 25 and 30 °C than at 15 and 33 °C. Increasing temperature shortened the longevity of both sexes but increased the intrinsic rate of increase (r_m) and finite capacity for increase (λ) with significantly shorter generation time (T) and doubling time (DT) within a temperature range of 15–30 °C. The net reproductive rate (R_0) was highest at 25 °C. Results of this study may improve our knowledge of fundamental biology and ecology in genus *Tarsonemus* in general and in *T. confusus* in particular. Based on the local climate conditions, the applications of these results in predicting the seasonal population dynamics of *T. confusus* and timing the pest management are discussed.

Keywords *Tarsonemus* mite · Temperature · Low temperature threshold · Life table parameter · Pest management

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Introduction

The genus *Tarsonemus* consists of more than 270 mite species (Lindquist 1986; Lin and Zhang 2002; Lofego et al. 2005; Magowski 2010), which are common in nature and can be collected from many plant species, leaf litter, fungi, soil and stored food products (Lindquist 1986; Zhang 2003). Most *Tarsonemus* mites are thought to be fungivorous (Lindquist 1986) and usually not considered as pests. However, some species, such as *Tarsonemus confusus* Ewing, occasionally occurring in greenhouses, can cause significant damage to plants when its population size is high (Zhang 2003). Van der Walt et al. (2011) report that in the Ceres area of South Africa, *Tarsonemus* species are dominant in apple developmental stages and have the highest incidence on mature fruit in all orchards, which are strongly associated with core rot diseases. Michailides et al. (1994) further show a high incidence of *T. confusus* on disease-infested fruits but not on healthy ones.

In China, bagging fruit 30–40 days after flowering is a prevalent technique applied in fruit production to prevent pest damage and pathogen infection, and reduce chemical application, in order to improve fruit quality and increase market access and price (Li et al. 2018). However, in the later 1990s and early 2000s, a disease with ‘black-dot’ symptoms on fruit broke out in the peach and apple orchards in North China where the fruit bagging technique was applied (Wang et al. 1999; Hao et al. 2007, 2010). Many pathogenic fungi, mainly the *Trichothecium roseum* (Persoon) Link, *Acremonium stritum* Gams and *Alternaria* spp., can be isolated from the injured pericarp or wounds of fruit, and these pathogens are weak parasitical and saprophytic fungi that cause symptoms only under moist conditions (Guo et al. 2005; Wang et al. 2014). Wang et al. (1999) assume that the presence of *T. confusus* and *Tarsonemus bilobatus* Sushii is a major cause of ‘black-dot’ symptoms. Hao et al. (2007, 2010) further provide evidence that symptoms on the bagged apple may be attributed to the presence of *T. confusus*. To reduce the impact of *T. confusus*, practicable methods including effective biological control (Li et al. 2018) or friendly chemical control should be applied to suppress *T. confusus* populations before fruit bagging. However, decisions regarding the appropriate time for the implementation of control methods highly depend on our knowledge of general biology of the target species, which is lacking in the genus *Tarsonemus* including *T. confusus*.

Temperature is one of the most important abiotic factors that drives the development of ectothermic organisms, such as insects and mites, and regulates their survival, reproduction, population growth and geographic distribution (Bale et al. 2002; Hance et al. 2007; Ristyadi et al. 2021, 2022). In ectotherms, as their body temperature fluctuates with the changing environmental temperature, the rates of biochemical reactions and biological processes inside their body increase exponentially with the increase of environmental temperature (Zuo et al. 2012). Ectotherms have an optimal thermal range in which they develop and reproduce (Block 1990; Chapman 1998). Within the optimal range, development is faster at higher temperatures because of the elevating development rate through the increasing metabolic rate (Corkett and McLaren 1970; Huey and Kingsolver 2011). However, above the optimal range, high temperatures induce slower development (Dillon and Frazier 2013) and higher mortality (Chapman 1998; Cooper and Cave 2016), whereas below the optimal range, low temperatures slow growth and reproductive rate, and below the lower threshold, these processes will cease (Block 1990; Cooper and Cave 2016). Moreover, because females have a finite amount of energy available for reproduction and survival during their lifespan, they have to make crucial decisions regarding the optimal allocation strategy to adopt the environmental changes.

In the present study, we investigated the life-history strategies of *T. confusus*, such as development, survival, reproduction and population growth, at various temperatures. Our results will improve our knowledge of fundamental biology in the genus *Tarsonemus* in general and in *T. confusus* in particular and provide information for analysis of pest risks and for decisions regarding the timing of management of this pest.

Materials and methods

Breeding colony

The breeding colony of *T. confusus* was established from adults collected from an apple orchard in 2012, in Changli County, Hebei Province, China. The colony was reared on wheat bran and maintained in a climate chamber (PRX-250C, Ningbo Saifu Experimental Instrument) at 25 ± 1 °C and $80 \pm 5\%$ RH in darkness.

Development, survival and reproduction

The thermal effect on the development, survival and reproduction of *T. confusus* was tested at six constant temperatures (i.e., 15, 20, 25, 30, 33 and 35 °C) and $70 \pm 5\%$ RH in darkness. There were 45 replicates (males or females) for each test temperature. Figure 1 shows the means of low, average and high temperatures in fields of the main apple growing regions in North, Northeast and Northwest China in 2014–2020 (WeatherSpark 2020).

To prepare mites for an experiment, one male and four female adults were randomly selected from the colony and transferred into a ‘chamber’ (i.e., a modified Munger cell) using a fine brush under a stereomicroscope (Leica EZ4, Germany). The chamber (16 mm diameter \times 4 mm depth) was made by drilling a whole in the centre of a piece of Plexiglas (76 mm length \times 25 mm width \times 5 mm height). After adults were transferred, the chamber was covered with a piece of glass (76 mm length \times 25 mm width \times 1–1.2 mm height). The Plexiglas and glass cover were clipped by two clamps to prevent mites from escaping. A total of 30 chambers were set up with five for each test temperature. Unless stated otherwise, a drop (0.05 mL) of PDA culture medium (i.e., 16.13% potato, 1.61% dextrose, 1.61% agar and 80.65% sterilized water, sterilized at 120 °C for 20 min) was dropped in

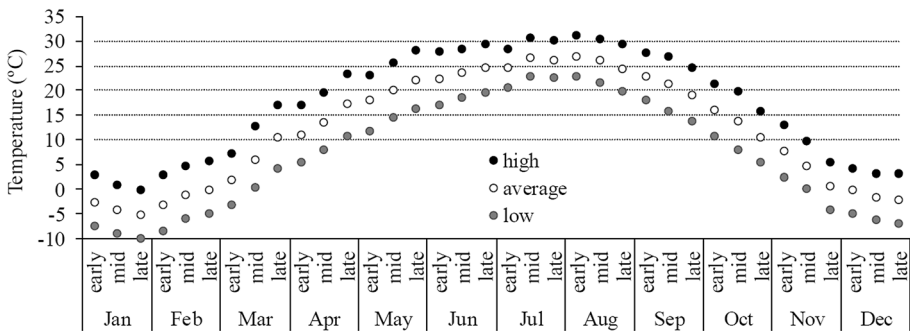


Fig. 1 Mean low, average and high temperatures in fields of the main apple growing regions in China in 2014–2018

the chamber and inoculated with fungi (*Fusarium* sp.) at least 1 day before experiment, serving as food for mites. Eggs laid in the chamber by the four females were allowed to hatch and develop to adults (second generation) under the same environmental conditions of the breeding colony. After emergence, one male and four female adults were randomly selected from different chambers and maintained in a new chamber until the females started oviposition, and they were then individually transferred into new chambers for oviposition.

To determine the development of *T. confusus*, newly laid eggs (< 6 h old) were individually transferred into new chambers (replicates) and maintained at a test temperature. The development and mortality of immature stages were checked daily and the developmental period of eggs, larvae and quiescent larvae and the period from eggs to adults were recorded. Newly emerged adults were sexed. Because mated females produced a female-biased sex ratio, eggs used to determine male development and mortality were laid by virgin females. The number of test mites varied between temperatures, life stages and sexes, i.e., $n=27-41$ and $29-45$, respectively, for male and female mortality, and $n=27-39$ and $17-39$, respectively, for male and female development.

To explore the effects of temperature on *T. confusus* reproduction and sex allocation, one male and one female (both < 6 h old) from the same test temperature were maintained in a chamber for 24 h, after which time adults were transferred into a new chamber. This process was repeated until they died. The eggs laid in each chamber were counted daily. Eggs were allowed to develop to adulthood and newly emerged adults were sexed. Longevity of both sexes was recorded. There were 39, 28, 28, 29 and 15 pairs tested for 15, 20, 25, 30 and 33 °C, respectively.

Statistical analysis

All data analyses were performed using SAS v.9.4 software (SAS Institute, Cary, NC, USA). Based on the developmental time at different temperatures, a linear regression (GLM procedure), $y=a+bT$, was fitted to the developmental rates vs. temperatures for each life stage, where y is the developmental rate, T the temperature, and a and b the estimated intercept and slope, respectively. The lower temperature threshold (T_0) for egg, larva, quiescent larva and immature (egg-adult) development was determined by extrapolating the regression line to the temperature axis (i.e., $T_0=-a/b$). The number of degree days (DD) above the T_0 required to complete development was estimated by the reciprocal of the slope (b) of the fitted regression line, i.e., $DD=1/b$. According to Campbell et al.

(1974), the standard error of T_0 is: $(\bar{y}/b) \times \sqrt{s^2/(N\bar{y}^2)} + (SE_b/b)^2$, where s^2 is the residual mean sum of squares of y , \bar{y} is the sample mean, SE_b is the standard error of slope b and N is the total number of samples. The standard error of DD is SE_b/b^2 . As mite development did not continuously accelerate when temperature increased to 33 °C, data collected at temperature from 15 to 30 °C only were used to estimate the T_0 and DD .

A likelihood-ratio test (log-binomial regression model, GENMOD procedure) was used to compare the immature mortality rate between temperatures and between sexes. A nonlinear regression model (NLIN procedure) fitting data that give exponential rise to maximum (Archontoulis and Miguez 2015) was used to estimate the cumulative proportion of eggs laid over time (day): cumulation of eggs laid (%) = $a \times (1 - e^{-b \times day})$, where a is the maximum value and b is a rate constant that determines the steepness of the curve. Another nonlinear regression model (NLIN procedure) fitting data with a unimodal distribution was applied to model the sexual allocation of *T. confusus* females over their age (day):

female offspring $\% = a/\{1 + [(day-b)/c]^2\}$, where a is the maximum value at age b and c is a rate constant of the curve. Data on adult survival were compared using a Wilcoxon test (LIFETEST procedure).

The normality of data on developmental period, number of eggs laid, number of female offspring produced, percentage of egg hatching, and percentage of female offspring was tested using a Shapiro–Wilk test (UNIVARIATE procedure) before analysis. Data on the number of female offspring produced were normally distributed and thus analysed by an ANOVA (GLM procedure) followed by Tukey’s studentized range test for multiple comparisons. Data on developmental period, number of eggs laid, egg hatch rate and proportion of female offspring were not normally distributed even after transformation, and hence analysed using a nonparametric ANOVA with Tukey’s studentized range test for multiple comparisons.

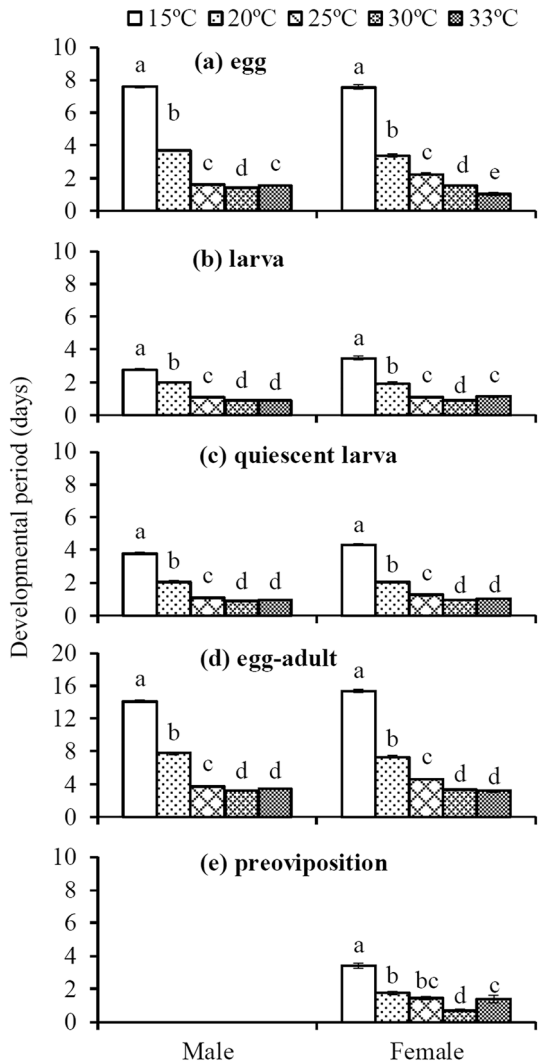
To estimate relative population growth of the mite and provide knowledge for the prediction of population dynamics, we calculated and compared their life table parameters using data on daily survival and reproduction using Jervis et al.’s (2005) method. The intrinsic rate of increase (r_m , females/female/day) was estimated by solving the Lotka–Euler equation, $\sum e^{-r_m x} l_x m_x = 1$, where x is the pivotal age, l_x is the proportion of females surviving to age x , and m_x is the number of female offspring produced per female at age x . Other life table parameters included the net reproductive rate ($R_0 = \sum l_x m_x$, females/females/generation), mean generation time [$T = \ln(R_0)/r_m$, days], doubling time [$Dt = \ln(2)/r_m$, days] and finite capacity for increase ($\lambda = e^{r_m}$). We used the bootstrap method (Yu et al. 2013) with 50,000 bootstrap samples to calculate the pseudo-values of life table parameters and applied the paired-bootstrap test (Efron and Tibshirani 1993; Reddy and Chi 2015) for multiple comparisons between any two temperatures (TTEST procedure). The significance was determined according to the 95% t-based confidence limits (95% CLs), i.e., if 95% CLs > 0 or < 0 , the mean difference between the two temperatures is significantly different ($P < 0.05$).

Results

No eggs hatched at 35 °C. As shown in Fig. 2, increasing temperature significantly shortened the developmental period of different life stages (male: $F_{4,156} = 326.39, 233.86, 271.24$ and 250.29 for egg, larva, quiescent larva and egg-adult, respectively; female: $F_{4,136} = 466.86, 190.25, 297.19$ and 531.45 for egg, larva, quiescent larva and egg-adult, respectively; all $P < 0.0001$) and the time period required by females to commence reproduction ($F_{4,135} = 108.10, P < 0.0001$), whereas the developmental period did not decrease significantly between 30 and 33 °C, except for that of female eggs (Fig. 2a).

Egg mortality was $< 10\%$ and was not significantly different between temperatures for each sex ($\chi^2 = 2.71$ and 3.52 for male and female, respectively, both d.f. = 4, $P > 0.05$) or between sexes for each temperature ($\chi^2 = 0.03, 3.79, 1.37, 0.08$ and 0.23 for 15, 20, 25, 30 and 33 °C, respectively, all d.f. = 1, $P > 0.05$) (Fig. 3a). For both sexes, mortality of larval, quiescent larval and egg-adult stages was usually higher at 33 °C than at other temperatures (larva: $\chi^2 = 21.63$ and 43.05 for male and female, respectively, both d.f. = 4, $P < 0.001$; quiescent larva: $\chi^2 = 9.45$ and 11.42 for male and female, respectively, both d.f. = 4, $P < 0.05$; egg-adult: $\chi^2 = 24.04$ and 30.91 for male and female, respectively, both d.f. = 4, $P < 0.0001$), with no significant difference between sexes for each temperature (χ^2

Fig. 2 Mean (\pm SE) developmental period (days) of *Tarsonemus confusus* males and females of different stages at five temperatures. Means within a sex and within a stage capped with the same letter are not significantly different (Tukey's studentized range test: $P > 0.05$)



< 3.81 , d.f. = 1, $P > 0.05$), expected at 33 °C where larva mortality of females was higher than that of males ($\chi^2 = 4.46$, d.f. = 1, $P = 0.035$) (Fig. 3b-d).

The calculated lower temperature threshold (T_0) and thermal requirement (i.e., degree days, DD) for males and females to start and complete development were similar (Table 1). Both sexes were expected to start development between 9.3 and 12.0 °C and the mites required about 60 DD to complete a life cycle. Females were likely to commence oviposition around 13 °C (Table 1).

The number of eggs laid and female offspring produced increased when temperature increased from 15 to 25 °C after which they declined ($F_{4,135} = 26.76$ and 26.38 for eggs and female offspring, respectively, both $P < 0.0001$) (Fig. 4a-b). Egg hatch rate was higher at 20, 25 and 30 °C than at 15 °C, and it was higher at 15 than at 33 °C ($F_{4,135} = 26.41$, $P < 0.0001$), with no significant difference found between 20, 25 and 30 °C (Fig. 4c).

Fig. 3 Immature mortality (%) of *Tarsonemus confusus* males and females of different stages at five temperatures. Columns within a sex and within a stage capped with the same letter are not significantly different (Likelihood-ratio test: $P > 0.05$)

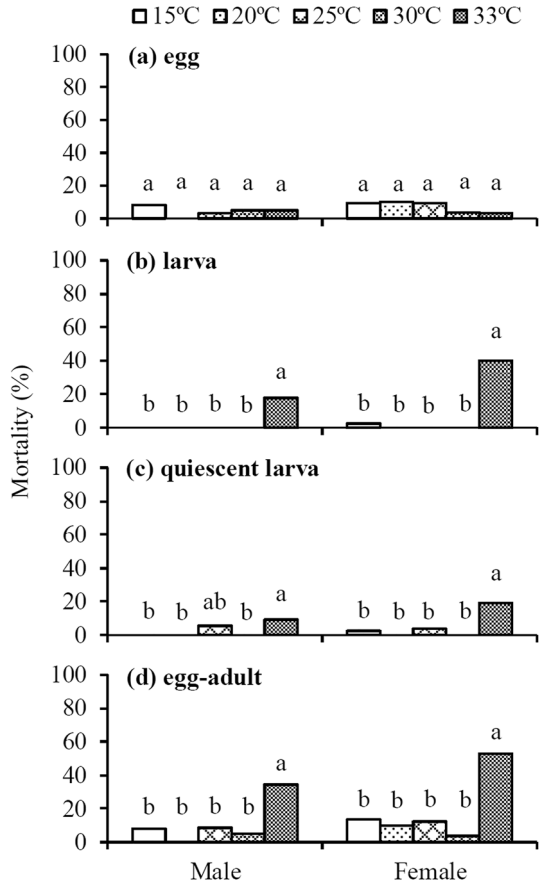


Table 1 Relationship between developmental rate (1/day, y) and temperature (T , °C), and estimated low temperature threshold (T_0 , °C) and degree days (DD) required to complete development of different stages of *Tarsonemus confusus*

Stage	Sex	Equation	R ²	F (df) ¹	T ₀	DD
Egg	Male	$y = -0.5094 + 0.0423 T$	0.8709	890.05 (1,132)	12.03 ± 0.20	23.62 ± 0.79
	Female	$y = -0.3890 + 0.0346 T$	0.9262	1531.59 (1,122)	11.26 ± 0.15	28.94 ± 0.74
Larva	Male	$y = -0.5381 + 0.0578 T$	0.6639	260.70 (1,132)	9.30 ± 0.36	17.29 ± 1.07
	Female	$y = -0.6221 + 0.0608 T$	0.7124	302.27 (1,122)	10.23 ± 0.34	16.44 ± 0.95
Quiescent larva	Male	$y = -0.7538 + 0.0665 T$	0.6850	287.00 (1,132)	11.34 ± 0.35	15.04 ± 0.89
	Female	$y = -0.6759 + 0.0601 T$	0.7971	479.38 (1,122)	11.25 ± 0.27	16.64 ± 0.76
Egg-adult	Male	$y = -0.1936 + 0.0174 T$	0.9053	1261.22 (1,132)	11.14 ± 0.16	57.57 ± 1.62
	Female	$y = -0.1716 + 0.0157 T$	0.9585	2816.08 (1,122)	10.97 ± 0.11	63.87 ± 1.20
Preoviposition	Female	$y = -1.2471 + 0.0967 T$	0.4249	90.14 (1,122)	12.90 ± 0.58	10.34 ± 1.09

¹ $P < 0.0001$ for all regression models

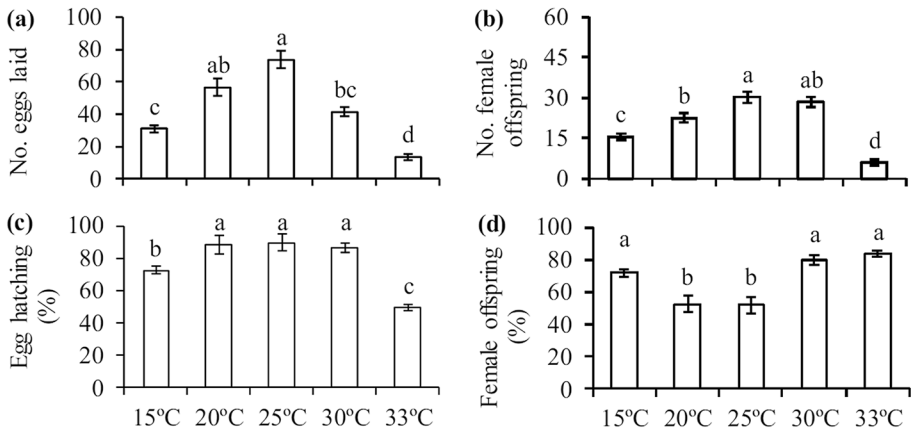


Fig. 4 Mean (\pm SE) number of eggs laid (a), number of female offspring produced (b), percentage of egg hatching (c), and percentage of female offspring (d) in *Tarsonemus confusus* at five temperatures. Means within a panel capped with the same letter are not significantly different (Tukey's studentized range test: $P > 0.05$)

The proportion of female offspring was lower at 20 and 25 °C than at other temperatures ($F_{4,135} = 17.31$, $P < 0.0001$) (Fig. 4d).

Increasing temperature significantly accelerated egg production, e.g., females completed reproduction early at higher temperatures (Fig. 5). Females laid 50% of eggs on day 20, 19, 12, 5 and 3 at 15, 20, 25, 30 and 33 °C, respectively (Fig. 5). With the increase of temperature, the proportion of female offspring peaked early during mothers' lifetime, i.e., 89% on day 15.4 at 15 °C, 99% on day 9.1 at 20 °C, 96% on day 5.3 at 25 °C and 89% on day 5.2 at 30 °C, whereas it continuously increased to 100% on day 7.0 at 33 °C (Fig. 6).

Males survived significantly longer at 15 °C than at other temperatures without significant differences detected between 20 and 25 °C or between 30 and 33 °C; male longevity was longer at 20 and 25 °C than at 30 and 33 °C ($\chi^2 = 129.66$, d.f.=4, $P < 0.0001$) (Fig. 7a). Females had similar longevity at 15 and 20 °C but they survived significantly longer than at 25 °C and the latter survived significantly longer than those at 30 and 33 °C ($\chi^2 = 141.49$, d.f.=4, $P < 0.0001$) (Fig. 7b). There was no significant difference in longevity between sexes at 15, 20 and 25 °C ($\chi^2 = 0.57$, 3.19 and 3.01 for 15, 20 and 25 °C, respectively, all d.f.=1, $P > 0.0001$); however, males survived significantly longer than females at 30 and 33 °C ($\chi^2 = 4.26$ and 6.83 for 30 and 33 °C, respectively, both d.f.=1, $P < 0.05$) (Fig. 7).

The r_m and λ significantly increased when the temperature increased from 15 to 30 °C then significantly decreased at 33 °C. Similarly, R_0 significantly increased when temperature increased from 15 to 25 °C then significantly decreased with increasing temperature (Table 2). T and Dt decreased significantly with increasing temperature, but Dt significantly increased again at 33 °C (Table 2).

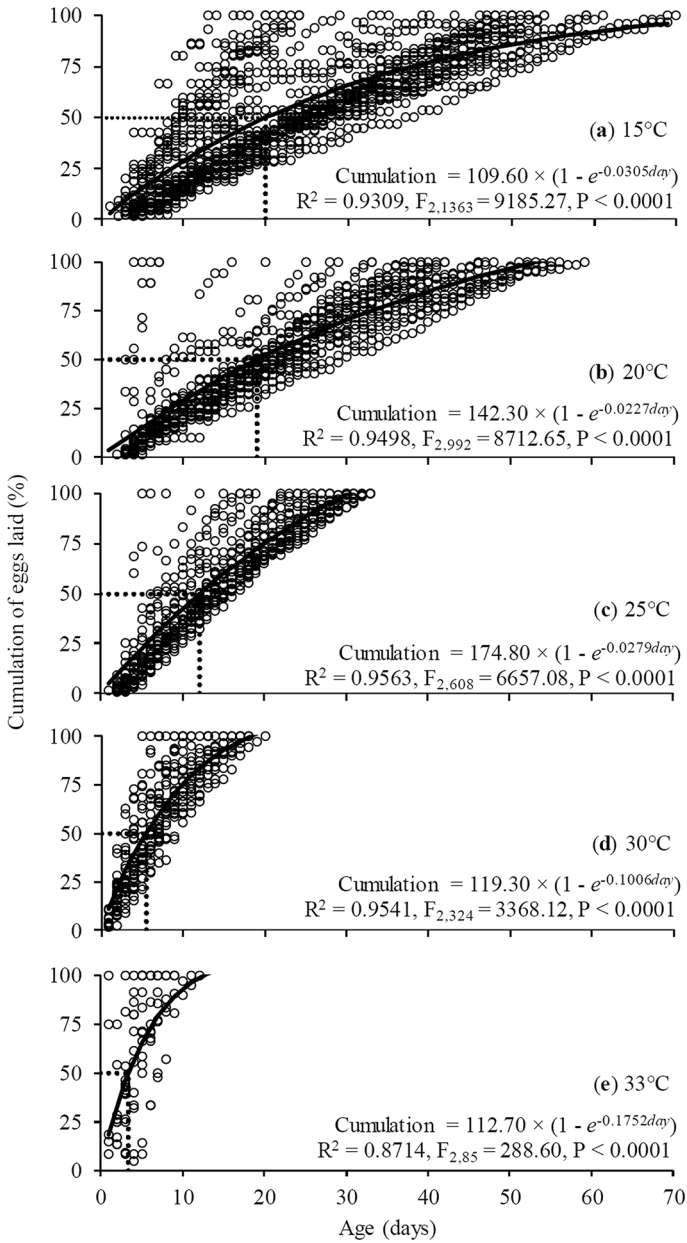


Fig. 5 Cumulative percentage of eggs laid by *Tarsonemus confusus* females at five temperatures. The vertical dotted lines indicate the age of females at which 50% of eggs were laid

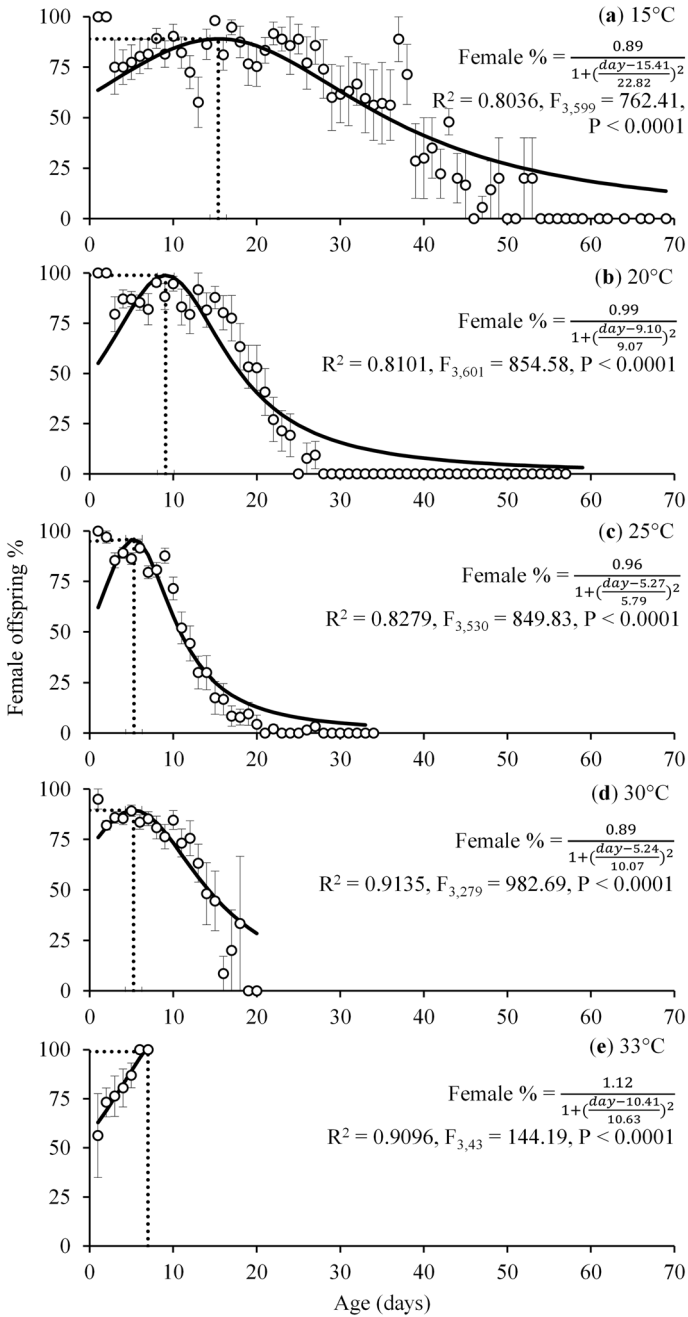


Fig. 6 Daily percentage of female offspring produced by *Tarsonemus confusus* females at five temperatures. The vertical dotted lines indicate the age of females at which the highest percentage of female offspring is produced

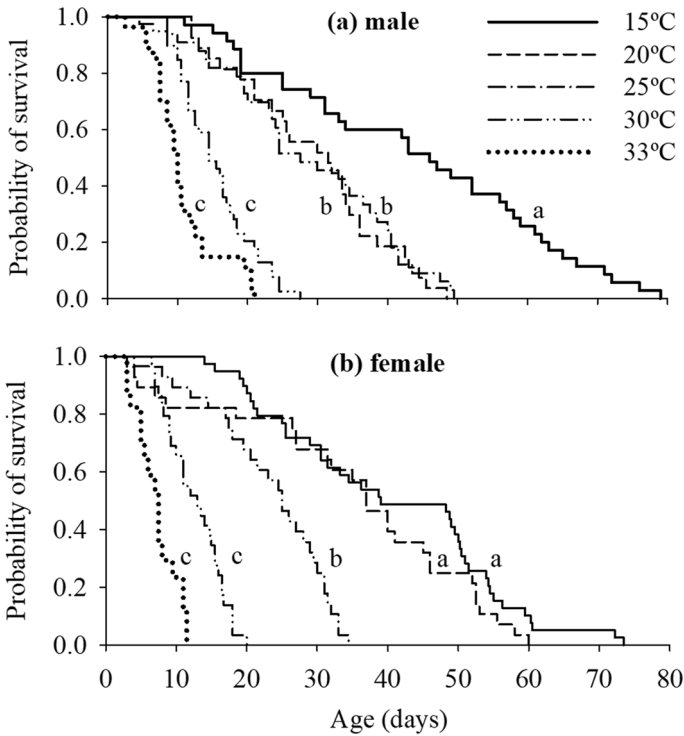


Fig. 7 Survival of *Tarsonemus confusus* male (a) and female (b) adults at five temperatures. Lines within a panel marked with the same letter are not significantly different (Wilcoxon test: $P > 0.05$)

Table 2 Mean (\pm SE) life table parameters of *Tarsonemus confusus* at five temperatures

Temperature ($^{\circ}$ C)	r_m	T	R_0	Dt	λ
15	0.1012 \pm 0.0000 e	27.09 \pm 0.02 a	15.51 \pm 0.03 d	6.85 \pm 0.00 a	1.1065 \pm 0.0001 e
20	0.2293 \pm 0.0005 d	13.71 \pm 0.03 b	23.21 \pm 0.08 c	3.02 \pm 0.01 b	1.2577 \pm 0.0006 d
25	0.3424 \pm 0.0007 b	10.00 \pm 0.02 c	30.72 \pm 0.07 a	2.02 \pm 0.00 d	1.4084 \pm 0.0010 b
30	0.3903 \pm 0.0000 a	8.60 \pm 0.01 d	28.69 \pm 0.07 b	1.78 \pm 0.00 e	1.4774 \pm 0.0000 a
33	0.3196 \pm 0.0033 c	5.99 \pm 0.03 e	6.78 \pm 0.10 e	2.17 \pm 0.02 c	1.3767 \pm 0.0045 c

Means within a column followed by a different letter are significantly different (i.e., 95% CLs > 0 or < 0 between any two temperatures)

Discussion

The response of ectotherms to surrounding temperature is important in understanding their life histories. Study on temperature-dependent phenology of pests permits examination of the impacts of temperature on the population dynamics, pest management and geographical distribution. A few studies have worked on the thermal requirements for the development and reproduction of pest mites in the family Tarsonemidae (e.g., Easterbrook

et al. 2003; Ferreira et al. 2006; Luypaert et al. 2014). So far, information is lacking for the genus *Tarsonemus*. As predicted by theory (Campbell 1974; Sharpe and DeMichele 1977; Block 1990; Chapman 1998; Knies and Kingsolver 2010) and reported by empirical studies (Ullah et al. 2011; Régnière et al. 2012; Zuo et al. 2012; Gotoh et al. 2015; Reed et al. 2017), our results show that when temperature increased from 15 to 25 or 30 °C, the developmental rate (Table 1, presented as a reciprocal of developmental time in Fig. 2), egg hatch rate, and reproductive potential in terms of fecundity and number of female offspring produced significantly increased; however, at 30 °C those parameters significantly decreased or at least did not continuously increase (Fig. 4a-c). These temperature-dependent response patterns pose a unimodal biological response of *T. confusus* over the test temperature range with an optimal temperature range being 20–30 °C for *T. confusus* development (Fig. 2) and reproduction (Fig. 4a-c).

Organisms develop and reproduce expending their reserved energy. The lower development rate, reproductive output and egg hatch rate at 15 °C in this study may be attributed to the inhibition of energy-demanding processes under cold environmental conditions (Pörtner 2002; Findsen et al. 2013). Our results show that eggs of *T. confusus* failed to hatch at 35 °C, females had significantly lower reproductive output and egg hatch rate was significantly lower at 33 °C. Because the rates of many processes that make up the resting metabolic rate (e.g., membrane turnover, protein turnover, ion homeostasis, and mitochondrial proton leak) increase at high temperatures, these processes may cause trade-offs with many repair mechanisms (Clarke 2006). Woods and Hill (2004) reported that in *Manduca sexta* (L.), increasing temperature will decline the diffusion of oxygen across the eggshell inducing the hypoxia in eggs. The oxygen limitation will trigger oxidative stress and finally lead to denaturation or malfunction of molecular repair as the protein synthesis is suspended (Pörtner 2002). This may also explain the significantly higher egg-adult mortality rate at 33 °C (Fig. 3c) and the significantly shorter lifespan of male and female adults of *T. confusus* at 30 and 33 °C (Fig. 7). The higher egg-adult mortality rate at 33 °C can be attributed to the lower survival rate at larval and quiescent larval stages (Fig. 3b-d). Moreover, females had significantly higher egg-adult mortality rate, suggesting that females were more sensitive to high temperatures than males (Fig. 3b-d).

Developmental time determines how fast organisms reproduce and their populations grow (Savage et al. 2004). With an increase of temperature from 15 to 30 °C, *T. confusus* females shortened their preoviposition period (Fig. 2e), increased reproductive rate (Fig. 5) and accelerated fertilization rate in a short period (Fig. 6), which may boost population growth with significantly increasing intrinsic rate of increase (r_m) and shorter generation time (T) and doubling time (DT) (Table 2). Results also indicate that population growth of *T. confusus* should be faster between 25 and 30 °C as indicated by the higher net reproductive rate (Table 2) due to the significantly greater number of female offspring produced (Fig. 4b) or more eggs fertilized during females' early life (Fig. 6). However, we found that a higher reproductive output at 20 and 25 °C (Fig. 4a) resulted in a lower proportion of female offspring (Fig. 4d), indicating that the females of *T. confusus* might have insufficient number of sperm available to fertilize more eggs, although they were individually paired with a male during their lifetime. In some species of mites, such as the two-spotted spider mite, *Tetranychus urticae* Koch, only sperm from the first mating will normally fertilize the eggs and the later matings usually are ineffective (Helle 1967). Similarly, Oku (2010) further reports that when the intervals between first and second copulation are more than 24 h, only the first copulation is effective for females. The effects of mating frequency and interval between matings on fertilization of *T. confusus* are not clear, future investigations into these aspects will help understand the sex allocation strategy of this species.

The estimated lower temperature thresholds for both sexes of *T. confusus* to complete development of preimaginal stages were between 9.3 and 12.0 °C and the mites required about 60 DD to complete a life cycle (Table 1). Therefore, it is expected that individuals of immature stages could be seen in the orchards in mid-March when the daytime temperature (i.e., high temperature) reaches up to 12.7 °C (Fig. 1; WeatherSpark 2020). However, Lindquist (1986) suggests that *Tarsonemus* mites overwinter primarily, if not exclusively, as adult females, which is demonstrated in *Tarsonemus fragariae* Zimmermann by Alford (1972). If this is the case for *T. confusus*, the presence of the first generation in spring is postponed to later March when the daytime temperature increases to 17.1 °C (Fig. 1; WeatherSpark 2020) which is higher than the low temperature threshold of 12.9 °C for female oviposition (Table 1). As the season progresses, the field populations of *T. confusus* will grow fast when mean temperature increases to 20.1 °C in mid-May with low and high temperatures of 14.5 and 25.7 °C, respectively (Fig. 2), and populations are expected to reach a maximum level between late June and late August when the low (i.e., 19.6–23.0 °C), mean (i.e., 24.3–27.0 °C) and high temperatures (i.e., 28.5–31.3 °C) (Fig. 1) fall in the optimal thermal range (i.e., 20–30 °C) (see Fig. 4a-c and Table 2). These ecological characteristics may enable *T. confusus* to build up the population and to break out during the growing seasons majorly from early April (flowering) to late October (harvest) when the average temperature is within the optimal thermal range for *T. confusus* development and reproduction in main apple growing regions in North, Northeast and Northwest China (WeatherSpark 2020). As fruit bagging is usually performed early-to-mid June (early summer) just before the establishment of maximum field populations of *T. confusus*, pest management via augmentative release of natural enemies (Li et al. 2018) or chemical spray should be implemented in mid- or late April (mid-spring) when the *T. confusus* populations are relatively small. However, it is well known that organisms react differently to fluctuating and constant temperatures (Vangansbeke et al. 2015), any expectation arisen from the results of laboratory experiments should be confirmed in field.

In conclusion, our results show that temperature has significant effects on the development, survival, oviposition, sex allocation and population growth of *T. confusus* with an optimal range detected between 20 and 30 °C. Based on the local climate conditions, the estimated lower temperature thresholds for immature development and female reproduction provide essential information to forecast the seasonal population dynamics. Further investigations into the overwintering strategies of *T. confusus* may provide more perceptive knowledge in predicting the presence of spring population, and studies on the development and reproduction of *T. confusus* on the bagged fruit will improve our understandings in the pest population growth and damage mechanisms in the fields. Moreover, the development of fruit bagging technology will enhance the efficiency of pest management, for example, the utilization of organic pesticides coated on the inner-layer of bags may efficiently reduce the population size of *T. confusus* or even eliminate the pests on the bagged fruit but needs further tests.

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Declarations

Competing interests The authors declare no competing interests.

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