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Article

Response to thermal environment in *Tetranychus ludeni* (Acari: Tetranychidae)

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Abstract

Tetranychus ludeni Zacher is a spider mite that has invaded all continents except Antarctica and become an economically important pest around the world. Understanding the plasticity of its life history traits as a response to temperatures provides critical information for its risk analysis and management. Here we tested its response to temperatures ranging from 15 to 30°C over two generations. We found that there was no difference in the egg hatch rate and immature survival rate across temperatures in the first generation. However, the egg hatch rate was lower and immature survival rate was higher at 30°C in the second generation. The sex ratio (proportion of females) of resultant adults was consistent under all test temperatures in both generations except for 30°C in the second generation which was lower. Higher temperature accelerated development in both generations but the development at the lower temperatures was faster in the second generation. Adult body size in both generations generally decreased with the increase of temperature, with females being more likely than males to adjust body size in response to temperature changes they first experienced. Temperature-dependent body size was not translated into fecundity, but larger adults lived longer. The thermal threshold was lower and degree days (DD) were greater in the second generation than in the first generation. Our findings indicate that life history traits of *T. ludeni* are highly flexible and adaptive to dynamic thermal environment in successive generations. Furthermore, increasing temperature elevated the intrinsic rate of increase (r_m) but shortened the generation time (T) and the time to double the population size (Dt). The net population growth rate (R_0) was higher at 20 and 25°C as compared to lower and higher temperatures.

Keywords: *Tetranychus ludeni*, temperature, life history traits, life table, adaptation

Introduction

Tetranychus ludeni Zacher is an invasive mite pest originating from Europe and now present in Asia, Africa, America, and Australasia (Migeon & Dorkeld 2018; CABI/EPPO 2020; Zhou *et al.* 2021). It attacks more than 250 plant species (Gotoh *et al.* 2015) including economically important crops such as carrots, beans, eggplants, pumpkins and other cucurbitaceous plants in warm regions and greenhouses of temperate areas (Zhang 2002; Adango *et al.* 2006; Fathipour & Maleknia 2016). Because temperature is a key factor influencing physiological processes in insects and mites (Ullah *et al.* 2010; Gotoh *et al.* 2015; Zou *et al.* 2018) and determining their distribution and abundance (Bale *et al.* 2002; Roy *et al.* 2002), global warming may further increase the distributional range of *T. ludeni* (Gotoh *et al.* 2015) and favor the spread of other invasive mites (Ghazy *et al.* 2019). Therefore, investigation into the influence of temperature on life history traits provides important information for pest risk analysis and management.

Evidence shows that egg hatch rate, immature survival, developmental time, adult longevity, and life table parameters vary substantially in different mite species and even different strains of the same species in response to test temperatures in the laboratory (e.g., Zhang *et al.* 1999; Da Silva

2002; Roy *et al.* 2003; Gotoh *et al.* 2010, 2015; Ullah *et al.* 2010; Riahi *et al.* 2013; Bazgir *et al.* 2015; Li *et al.* 2015; Liu & Zhang 2016; Bayu *et al.* 2017; Zou *et al.* 2018; Hasanvand *et al.* 2019; Ristyadi *et al.* 2019). This may be attributed to a diverse range of physiological limits in different species (Nguyen *et al.* 2014) and adaptation to temperature changes in different strains (Gotoh *et al.* 2010). However, most studies on the effect of temperature on mite life history traits analyze their data from only one generation, making it difficult to evaluate mites' potential adaptations to variations of temperature over generations. Hence, examination of life history traits in response to different temperatures for more than one generation can provide information on how mites may adapt to dynamic thermal environment for prediction of their potential of invasions and crop damage in the world.

Temperature is also an important factor regulating sex ratio in spider mites (e.g., De Moraes & McMurtry 1987; Margolies & Wrensch 1996; Roy *et al.* 2003; Gotoh *et al.* 2015). Roy *et al.* (2003) suggest that females have better capacities than males to disperse and survive under harsh conditions in some spider mite species, such as *T. mcdanieli* McGregor, and consequently, their sex ratio should be increasingly female-biased at extremely low or high temperatures indicating deteriorating habitats. Yet, it is largely unknown whether this notion applies to other spider mites. Furthermore, body size of adults developing from immatures at different temperatures may vary substantially (Klok & Harrison 2013). For example, body size of geographic strains of a species in warmer regions should be smaller than in cooler regions (Walters & Hassall 2006; Plesnar-Bielak *et al.* 2013; Pequeno *et al.* 2018). However, it is not clear whether such temperature-dependent body size is translated into fecundity in spider mites.

In the present study, we aimed to investigate the life history strategies of *T. ludeni* in response to dynamic thermal conditions in two successive generations. Based on theoretic framework and empirical findings outlined above, we postulate that (1) higher temperature accelerates development and shortens adult longevity; (2) immature mortality is higher and sex ratio is more female-biased at low and high temperatures; (3) adults that develop from lower temperatures are larger and more fecund, and (4) mites can adapt to thermal changes over generations. To test these hypotheses, we carried out a series of experiments and compared various life history traits in response to dynamic temperatures within and between generations. We also created a life table using data collected.

Materials and Methods

Breeding colony and test temperatures

We established a breeding colony of *T. ludeni* from field collected adults on *Passiflora mollissima* (Kunth) (Malpighiales: Passifloraceae) in Palmerston North, New Zealand. We maintained the colony on 20 potted kidney bean plants [*Phaseolus vulgaris* L. (Fabales: Fabaceae)] at $25 \pm 1^\circ\text{C}$ temperature and 50 ~ 70% RH with a photoperiod of 16L:8D hours. We replaced the 10 oldest plants fortnightly with new ones by cutting leaves of old plants with mites on and placing them on the top of new plants. We tested effects of four temperatures (15, 20, 25, and $30 \pm 1^\circ\text{C}$) under the above RH and photoperiod conditions using four growth chambers (I-36VL, Percival Scientific Inc., Perry, Iowa, USA).

Effect of temperature on life history traits

To determine whether survival, development and reproduction of *T. ludeni* responded to the same temperature treatments differently in different generations, we exposed mites to the above test temperatures for two generations and recorded egg hatch, immature survival and developmental time between oviposition and adult emergence, and sex ratio and body size of resultant adults. The first

generation started from the eggs laid by mites from the breeding colony and the second generation commenced from the eggs produced by the first generation.

We performed 20 replicates per temperature treatment in each generation. For each replicate, we put 50 eggs on a bean leaf disc (3 cm × 3 cm) laid by mated females of ≤ 1-d-old at a test temperature. We placed the leaf disc (3 cm × 3 cm) upside down on a water saturated cotton pad in a Petri dish (5.5 cm diameter × 1.0 cm height) during the entire treatment period. We replaced leaf discs with fresh ones once every five days and examined each leaf disc daily until all individuals reached adult stage. We randomly selected two females and two males of resultant adults per replicate for body size measurement (area from top view) under a digital camera (Olympus SC30, Japan) connected to the stereomicroscope and a computer with Adequate Imaging software (CellSens® GS-ST-V1.7, Olympus, Germany) installed.

To determine fecundity and adult longevity, we randomly selected 20 newly emerged females and 20 newly emerged males from each of the above treatments in the first generation and individually paired them on a leaf disc (2 cm × 2 cm) in a Petri dish as mentioned above. Twenty-four hours after pairing, we individually transferred males onto clean leaf discs of the same size in Petri dishes and replaced leaf discs once every three days until males died. We allowed females to stay on the same leaf discs for three days, after which time, we individually transferred them onto new leaf discs of the same size in Petri dishes. We repeated this process until females died. We counted the number of eggs laid by each female and monitored adult longevity daily. Due to logistical reasons we did not estimate the above parameters for the second generation.

We calculated the life table parameters (Jervis *et al.* 2005) for each temperature by using the above data collected in the first generation. The intrinsic rate of increase (r_m , daughters/female/day) was calculated by solving the Lotka-Euler equation, $\sum e^{-r_m x} l_x m_x = 1$, where x is the pivotal age of females, l_x is the proportion of females surviving to age x , and m_x is the number of daughters produced per female at age x . We also estimated other life table parameters, including the net reproductive rate ($R_0 = \sum l_x m_x$, daughters/female/generation), mean generation time [$T = \log_e(R_0)/r_m$, days], and doubling time [$Dt = \log_e(2)/r_m$, days]. For each treatment, a jackknife method (Caswell 2001) was used to estimate the life table parameters for each female.

Statistical analysis

We tested the distribution of data using a Shapiro-Wilk test (UNIVARIATE procedure) and used SAS 9.3 (SAS Institute 2011) to analyze all data. Data on the male and female adult body size, and $\ln(x)$ -transformed number of eggs laid and developmental period were normally distributed and thus analyzed using an mixed-factor analysis of variance (ANOVA, GLM procedure) followed by Tukey's Studentized range test for multiple comparisons. Data on egg hatch, immature survival, sex ratio (proportion of females) of resultant adults and life table parameters were not normally distributed even after transformation, and thus analyzed using a non-parametric mixed-factor ANOVA (GLM procedure). Data on adult survival were compared using a Wilcoxon test (LIFETEST procedure).

To determine the low temperature threshold (T_0) and degree-days (DD) required to start and complete development of immature stages, we fitted the developmental rates ($y = 1/\text{developmental time}$) over temperatures (T) using a linear regression (GLM procedure): $y = a + bT$, where a and b are estimates of the y intercept and slope, respectively. We then calculated $T_0 = -a/b$, and $DD = 1/b$. According to Campbell *et al.* (1974), the standard errors of T_0 and DD were calculated as $(\bar{y}/b)\sqrt{s^2/(N\bar{y}^2) + (SE_b/b)^2}$ and SE_b/b^2 , respectively, where s^2 is the residual mean sum of square of y , \bar{y} the sample mean, SE_b the standard error of slope b , and N the total number of samples.

Results

We show that proportions of eggs that hatched and immatures that survived to adults and sex ratio of resultant adults were largely similar across test temperatures in both generations (Figure 1). The only difference occurred at 30°C in the second generation where egg hatch rate was significantly lower than at 25 and 30°C in the first generation ($F = 3.21$; $df = 7, 149$; $P = 0.0034$) (Figure 1A), immature survival rate was significantly higher than at 15°C in the first generation ($F = 2.59$; $df = 7, 148$; $P = 0.0125$) (Figure 1B), and the proportion of resulting females was significantly lower than all other treatments in both generations ($F = 8.68$; $df = 7, 141$; $P < 0.0001$) (Figure 1C).

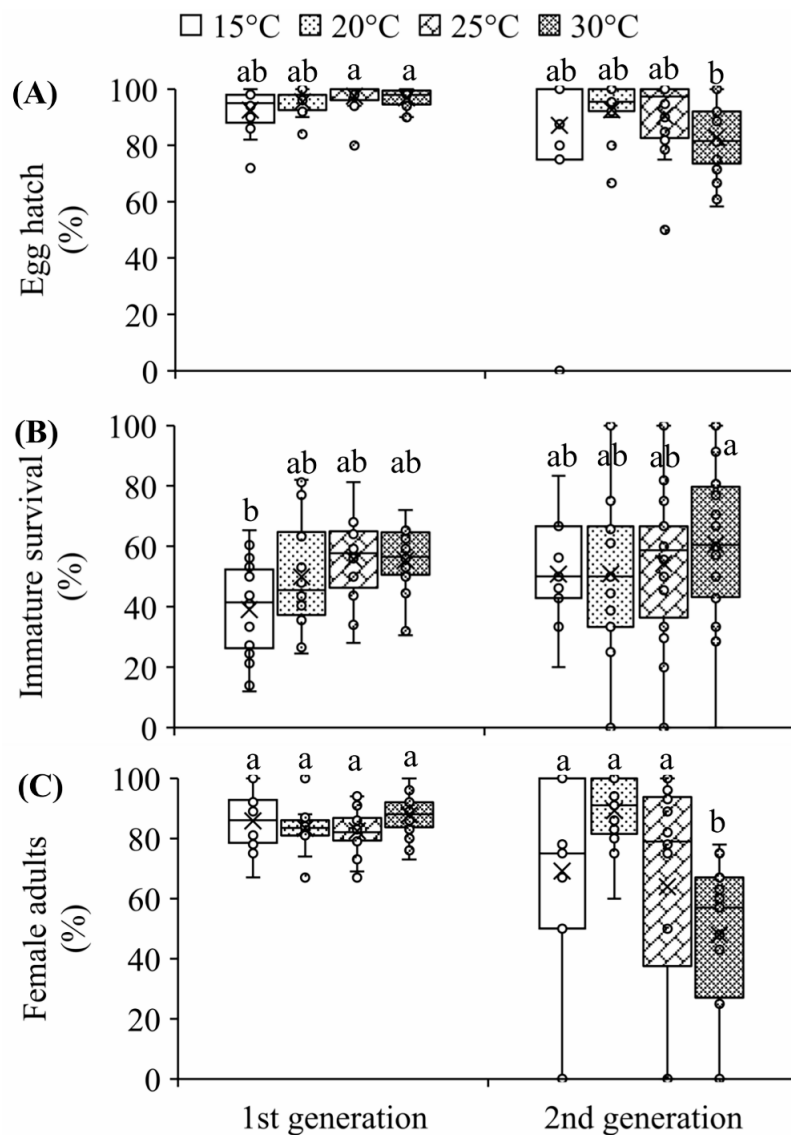


FIGURE 1. Mean (\pm SE) percentage of egg hatch (A), immature survival (B) and resulting female adults (C) at different temperatures in the first and second generations in *T. ludeni*. Columns with the same letters are not significantly different ($P > 0.05$). For each box plot, the upper and lower box lines represent 75% and 25% of scores falling beyond the upper and lower quartiles, respectively; the 'x' and line in a box indicate the mean and median score, respectively; the 'T' and 'L' are the upper and lower whiskers showing scores outside the 50% middle; the circles are the outliers of scores.

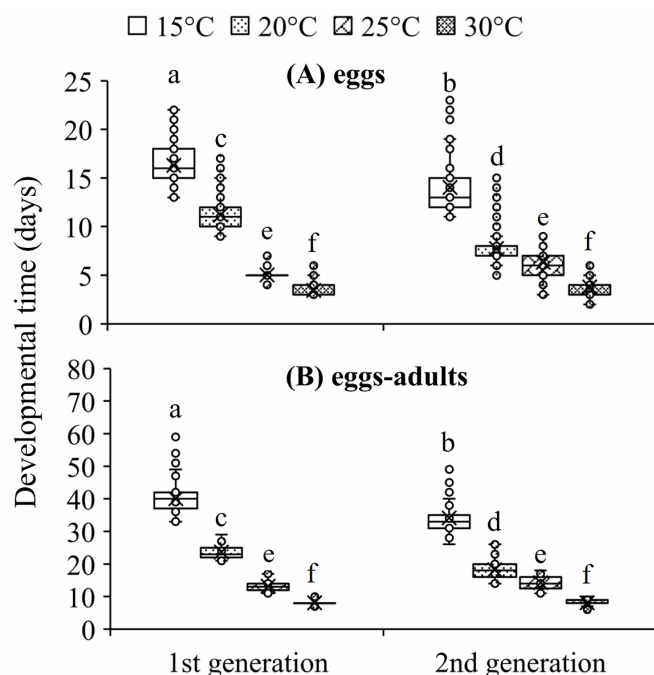


FIGURE 2. Mean (\pm SE) developmental time of eggs (A) and from eggs to adults (B) at different temperatures in the first and second generations in *T. ludeni*. Columns with the same letters are not significantly different ($P > 0.05$). For each box plot, the upper and lower box lines represent 75% and 25% of scores falling beyond the upper and lower quartiles, respectively; the ‘×’ and line in a box indicate the mean and median score, respectively; the ‘┌’ and ‘└’ are the upper and lower whiskers showing scores outside the 50% middle; the circles are the outliers of scores.

Tetranychus ludeni significantly accelerated their development with the increase of temperature in both generations, with the second generation developing significantly faster at 15°C and 20°C than the first generation ($F = 7341.52$; $df = 7, 4770$; $P < 0.0001$ for eggs, and $F = 9463.52$; $df = 7, 2443$; $P < 0.0001$ for egg-adult) (Figure 2). Adult body size of both sexes generally decreased significantly with the increase of temperature from 20°C in both generations with it being the largest at 20°C and smallest at 30°C ($F = 30.30$; $df = 7, 263$; $P < 0.0001$ for females, and $F = 13.34$; $df = 7, 219$; $P < 0.0001$ for males) (Figure 3). Although the developmental rate and temperature were significantly positively correlated in both generations, the low temperature threshold (T_0) was lower and degree days (DD) were greater in the second generation than in the first generation (Table 1).

Table 1. Relationship between developmental rate ($1/d$, y) and temperature (T , °C), and the estimated mean (\pm SE) low temperature threshold (T_0 , °C) and degree day (DD) required to start and complete development of eggs and from egg to adult stage in *T. ludeni*.

Stage	Equation	R^2	$F_{(df)}$	P	T_0	DD
<i>1st generation</i>						
Egg	$y = -0.2064 + 0.0164T$	0.8807	28221.50 _(1,2695)	< 0.0001	12.56 \pm 0.03	60.85 \pm 0.36
Egg-adult	$y = -0.0864 + 0.0068T$	0.9291	25085.60 _(1,1913)	< 0.0001	12.72 \pm 0.03	147.15 \pm 0.93
<i>2nd generation</i>						
Egg	$y = -0.1315 + 0.0132T$	0.4043	1466.21 _(1,960)	< 0.0001	10.23 \pm 0.13	75.62 \pm 1.98
Egg-adult	$y = -0.0749 + 0.0064T$	0.7896	2003.54 _(1,534)	< 0.0001	11.70 \pm 0.11	156.28 \pm 3.49

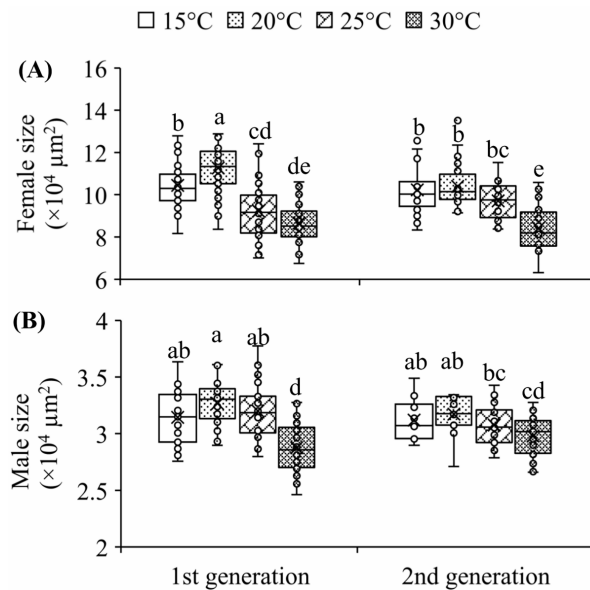


FIGURE 3. Mean (\pm SE) body size of female (A) and male adults (B) in *T. ludeni* at different temperatures. Columns with the same letters are not significantly different ($P > 0.05$). For each box plot, the upper and lower box lines represent 75% and 25% of scores falling beyond the upper and lower quartiles, respectively; the 'x' and line in a box indicate the mean and median score, respectively; the 'T' and '┴' are the upper and lower whiskers showing scores outside the 50% middle; the circles are the outliers of scores.

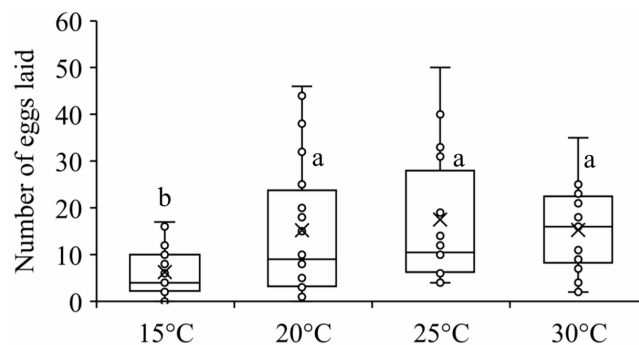


FIGURE 4. Mean (\pm SE) number of eggs laid by females during their lifetime at different temperatures in *T. ludeni*. Columns with the same letters are not significantly different ($P > 0.05$). For each box plot, the upper and lower box lines represent 75% and 25% of scores falling beyond the upper and lower quartiles, respectively; the 'x' and line in a box indicate the mean and median score, respectively; the 'T' and '┴' are the upper and lower whiskers showing scores outside the 50% middle; the circles are the outliers of scores.

In the first generation, lifetime fecundity of females that developed from 15°C was significantly lower than that from other treatments ($F = 4.34$; $df = 3, 76$; $P = 0.0071$) where fecundity was similar (Figure 4). Adult males had similar longevity at 15 and 20°C but their longevity significantly decreased with the increase of temperature from 20 to 30°C ($\chi^2 = 52.88$; $df = 3$; $P < 0.0001$) (Figure 5A). Adult females survived significantly longer at 20°C than at 15 and 25°C, and their longevity was the shortest at 30°C ($\chi^2 = 83.29$; $df = 3$; $P < 0.0001$) (Figure 5B). As shown in Table 2, increasing temperature significantly elevated the intrinsic rate of increase (r_m) but significantly shortened the generation time (T) and the time to double the population size (D_t). The net population growth rate (R_0) was significantly higher at 20 and 25°C as compared to lower and higher temperatures.

TABLE 2. Mean (\pm SE) life table parameters of *T. ludeni* at different temperatures.

Temperature ($^{\circ}$ C)	r_m	R_0	T	Dt
15	0.0219 \pm 0.0001 d	1.95 \pm 0.02 d	30.35 \pm 0.39 a	31.64 \pm 0.22 a
20	0.0722 \pm 0.0001 c	6.85 \pm 0.09 a	26.61 \pm 0.16 b	9.60 \pm 0.02 b
25	0.1009 \pm 0.0005 b	6.55 \pm 0.10 b	18.60 \pm 0.11 c	6.87 \pm 0.04 c
30	0.1281 \pm 0.0010 a	4.00 \pm 0.05 c	10.81 \pm 0.05 d	5.42 \pm 0.04 d
$F_{(df)}$	389.44 _(3,76)	171.55 _(3,76)	302.75 _(3,76)	389.44 _(3,76)
P	< 0.0001	< 0.0001	< 0.0001	< 0.0001

Means followed by different letters in columns are significantly different ($P < 0.05$).

Discussion

We show that the egg hatch rate in the New Zealand strain of *T. ludeni* was $> 95\%$ without significant difference between test temperatures from 15–30 $^{\circ}$ C in the first generation (Figure 1A). Our finding agrees to that for the Japanese strain exposed to similar temperature range for one generation (Gotoh *et al.* 2015). However, the hatch rate was significantly lower at 30 $^{\circ}$ C in the second generation than at 25 $^{\circ}$ C and 30 $^{\circ}$ C in the first generation (Figure 1A), indicating that exposure to 30 $^{\circ}$ C for more than one generation would reduce egg survival in *T. ludeni*. Immature survival remained similar across test temperatures in the first generation but was higher at 30 $^{\circ}$ C in the second generation (Figure 1B). This could be an adaptive strategy to compensate lower hatch rate at 30 $^{\circ}$ C in the second generation.

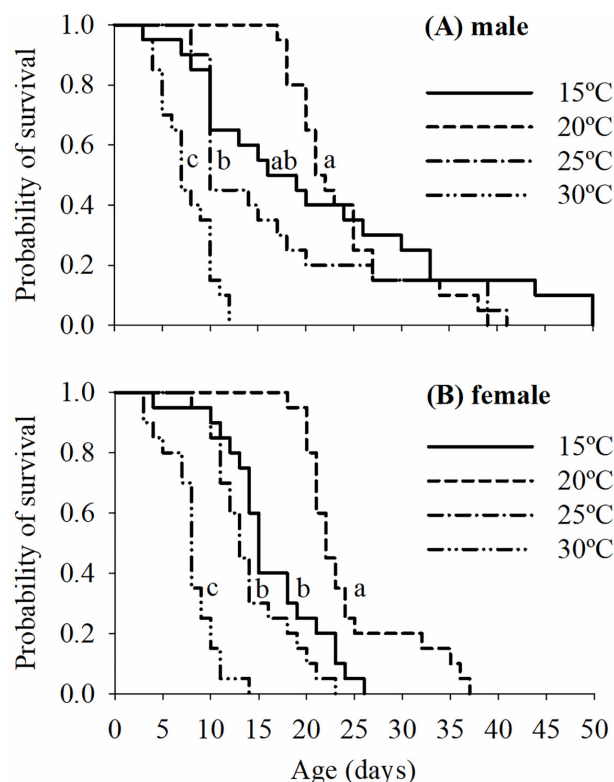


FIGURE 5. Survival of male (A) and female adults (B) at different temperatures in *T. ludeni*. Lines with the same letters are not significantly different ($P > 0.05$).

Like other haplodiploid species including spider mites (Roy *et al.* 2003; Macke *et al.* 2011; Tamura & Ito 2017), *T. ludeni* generally had a female-biased sex ratio across our test temperatures (Figure 1C). Based on the data from one generation, the sex ratio (proportion of female adults) is higher at 30°C than at lower temperatures in the Japanese strain of *T. ludeni* (Gotoh *et al.* 2015) and it is more female-biased in *T. mcdanieli* at 15°C and 34°C as compared to temperatures between 20°C and 32°C (Roy *et al.* 2003). Roy *et al.* (2003) suggest that the increased female-biased sex ratio at extreme temperatures may be an evolutionary response to deteriorating habitats because tetranychid females appear to have better abilities than males to disperse and survive under harsh conditions. However, our findings show that the sex ratio was consistent across all test temperatures in both generations except for 30°C in the second generation which was significantly lower (Figure 1C). The higher immature survival (Figure 1B) and lower sex ratio (Figure 1C) at 30°C in the second generation may be an adaptive response to higher temperature over generations in *T. ludeni*.

Similar to reports on *T. ludeni*'s Japanese strain (Gotoh *et al.* 2015) and other mite species (Margolies & Wrensch 1996; Da Silva 2002; Bazgir *et al.* 2015; Li *et al.* 2015; Zou *et al.* 2018), we found that the New Zealand strain of *T. ludeni* developed significantly faster with the increase of temperature from 15 to 30°C in both generations (Figure 2), supporting the notion that increasing temperature elevates metabolic rate and thus shortens developmental time (Woods & Hill 2004; Potter *et al.* 2009; Schulte 2015). However, compared to the first generation, the second generation developed faster at 15°C and 20°C (Figure 2). These findings suggest that *T. ludeni* can adjust its developmental period based on its experience in the previous generation. Adaptation to thermal environment over successive generations is also reported in the predatory mite *Amblydromalus limonicus* Garman and McGregor (Acari: Phytoseiidae) (Walzer *et al.* 2020). We propose that *T. ludeni* accelerates its development at lower temperatures to promote an early start of reproduction after experiencing longer development and delayed reproduction in the first generation at these lower temperatures.

We demonstrate that *T. ludeni* adult body size in both generations (Figure 3) followed the so-called temperature-size rule where body size decreases with the increase of environmental temperature, as reported in many ectotherms (Atkinson 1994; Walters & Hassall 2006; Klok & Harrison 2013; Pequeno *et al.* 2018). However, the degrees and patterns of size changes in response to temperature differed between sexes as well as between generations. For example, the degree of size variation was greater in females than in males in the first generation while size changes of both sexes were smaller in the second generation (Figure 3). These findings have two implications: (1) females are more likely than males to adjust body size in response to temperatures they first experience, and (2) both sexes can adapt to temperatures they have experienced in the previous generation.

We found that temperature-dependent female body size did not translate into fecundity in *T. ludeni* because females that developed from 15–20°C were larger than those from higher temperatures (Figure 3A) but females from 15°C laid fewer eggs than those from higher temperatures where there was no difference (Figure 4). These findings differ from those for the Japanese strain where highest and lowest fecundity occurs at 20°C and 30°C, respectively (Gotoh *et al.* 2015) and for the Brazilian strain where females lay greatest number of eggs at 30°C (Da Silva 2002). In *T. urticae*, Riahi *et al.* (2013) and Zou *et al.* (2018) report the highest fecundity at 25°C and 28°C, respectively. Our results indicate that temperature-dependent adult body size was associated with longevity and such association was different between sexes (Figures 3 and 5). In the first generation, larger male body size at 15–20°C (Figure 3B) translated into longer longevity at the same temperature range (Figure 5A) while females had largest body size (Figure 3A) and longest longevity (Figure 5B) at 20°C. In several other mite species (Riahi *et al.* 2013; Sugawara *et al.* 2017) and the Japanese strain of *T. ludeni* (Gotoh *et al.* 2015), longevity decreases with the increase of temperature.

In this study, the lower thermal threshold (T_0) and degree days (DD) for *T. ludeni* development from eggs to adults (Table 1) fell within the range from 7.8 to 13.8°C and from 110 to 156 DD, respectively, reported for the genus *Tetranychus* for one generation (Sakunwarin *et al.* 2003; Gotoh *et al.* 2010, 2015; Ullah *et al.* 2010; Karami-Jamour and Shishehbor 2012; Riahi *et al.* 2013; Bayu *et al.* 2017; Hasanvand *et al.* 2019). The varying thermal requirements for development between species or strains of the same species probably reflect their adaptations to the local climate (Gotoh *et al.* 2015). Although the developmental rate and temperature were significantly positively correlated in both generations, T_0 was lower and degree day (DD) was greater in the second generation than in the first generation (Table 1). These results also suggest that *T. ludeni* can adapt to temperature changes by adjusting its developmental rate based on its experience in the previous generation. The life table shows that the intrinsic rate of increase (r_m) increased and doubling time (Dt) decreased with the increase of temperatures from 15 to 30°C (Table 2). These may be attributed to the shorter developmental time (Figure 2) and more daughters produced during the females' early lifespan at higher temperatures (DR unpublished data). Because population size has a significant effect on reproduction and population growth in *T. ludeni* (Weerawansa *et al.* 2020), the population size changes in response to temperatures can further facilitate its invasion success.

In conclusion, life history traits of *T. ludeni* are highly flexible and adaptive to dynamic thermal environment over generations. We show that higher temperature accelerates its development in both generations, but the development at the lower temperatures is faster in the second than in the first generation. This suggests that the mite shortens its developmental time at lower temperatures in the second generation to promote an early start of reproduction after experiencing longer development and delayed reproduction in the first generation at these temperatures. Adult body size in both generations decreases with the increase of temperature, with females being more likely than males to adjust body size in response to temperature changes they first experience. Larger body size results in greater longevity but not higher fecundity. Lower thermal threshold and greater degree days (DD) in the second generation than in the first generation suggest that *T. ludeni* can adapt to temperature changes by adjusting its developmental rate based on its experience in the previous generation.

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