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Dynamics of life history traits in *Tetranychus ludeni* Zacher in response to fluctuating temperatures

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Tetranychus ludeni Zacher (Acari: Tetranychidae) is an invasive spider mite that currently occurs in Europe, Asia, Africa, America, and Australasia (CABI 2011; Migeon & Dorkeld 2018). It feeds on more than 300 plant species in 60 families and causes significant damage to a number of economically important crops such as eggplant, pepper, tomato, bean, pumpkin and other cucurbitaceous plants (Zhang 2002, 2003; Gotoh *et al*. 2015). In their study on effects of constant temperatures on several spider mite species, Gotoh *et al.* (2015) suggest that *T. ludeni* may be better adapted to warmer climate and predict that it could replace *T. urticae* to become a major pest of crops in the world. However, temperature in nature is fluctuating, typically higher during the daytime and lower during the nighttime, which could have different effects on organisms (Fischer *et al.* 2011; Paaijmans *et al*. 2013; Bowden *et al.* 2014; Gotoh *et al*. 2014; Zeh *et al.* 2014; Nachman & Gotoh 2015; Bayu *et al*. 2017). So far, how fluctuating thermal conditions affect life history traits of *T. ludeni* is unknown. In the present study, we investigated the plasticity of life history traits in response to fluctuating temperatures in *T. ludeni* to provide information for predicting its potential to invade and to become a major pest in different regions or conditions.

We maintained a breeding colony of *T. ludeni* on 20 potted kidney bean plants (*Phaseolus vulgaris* L.) in the Massey University Entomology and IPM Laboratory, Palmerston North, New Zealand, at 25 ± 1°C temperature and 50 ~ 70% RH with a photoperiod of 16L:8D hours. We performed four fluctuating temperature treatments (15~21, 22~28, 29~35 and 36~42°C) with 20 replicates per treatment in growth chambers (I-36VL, Percival Scientific Inc., Perry, Iowa, USA). The temperature setting protocol is shown in Figure 1. For each replicate, we randomly collected 20 female and 4 male adults from the colony, introduced them onto a bean leaf disc (3 cm × 3 cm) placed upside down on a water saturated cotton pad in a Petri dish (5.5 cm diameter × 1.0 cm height), and allowed them to stay on the leaf disc for 24 hours at 25°C. We kept 50 eggs on the leaf disc, removed the redundant eggs using a soft paintbrush, and then placed the Petri dish with 50 eggs into a growth chamber at a test temperature. We replaced the leaf disc with a fresh one once every five days. We took each Petri dish from the test temperature once a day for a few minutes and recorded egg hatch, immature stage mortality and adult emergence under a stereomicroscope (Leica MZ12, Germany) at 25°C. During the few minute's observation each day, we also sexed and removed emerged adults and recorded development period (from egg to adulthood) of each sex.

To determine the effect of treatments on adult body size, we randomly selected two females and two males of the resultant adults per replicate and measured their size under a digital camera (Olympus SC30, Japan) connected to the stereomicroscope and a computer with adequate imaging software (CellSens® GS-ST-V1.7, Olympus, Japan) installed. To obtain information on the effect of treatments on reproductive outputs and adult longevity, we randomly selected 20 newly emerged females and 20 newly emerged males (< 1 d old) from each of the above treatments and individually

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paired them on a leaf disc (2 cm × 2 cm) in a Petri dish as mentioned above. We maintained all these adults under the same treatment conditions. Twenty-four hours later, we transferred the male to a clean leaf disc of the same size in another Petri dish and recorded its longevity. We allowed the female to lay eggs for 72 hours on the same leaf disc and then transferred her to a new leaf disc of the same size in another Petri dish. We repeated this process until her death, and recorded fecundity and egg hatch rate of all eggs laid by each female. Mite transfer, and fecundity and egg hatch recording were performed at 25°C for a few minutes.

All data were analysed using SAS 9.4 with a rejection level set at α < 0.05. A Shapiro-Wilk test (UNIVARIATE procedure) was used to test the distribution of data. Data on the immature survival rate, and male and female adult body size were normally distributed and thus analysed using an analysis of variance (ANOVA, GLM procedure) followed by Tukey's Studentized range test. Data on the number of eggs laid were $\ln(x)$ transformed to achieve normal distribution before ANOVA. Data on egg hatch rate, and offspring sex ratio and developmental period were not normally distributed even after transformation, and thus analysed using a non-parametric ANOVA (GLM procedure) with a Tukey test for multiple comparisons. Data on adult survival were compared using a Wilcoxon test (LIFETEST procedure).

Our results show that no eggs hatched at the treatment of 36~42ºC, indicating that this temperature range is lethal to *T. ludeni* eggs. Similarly, Gotoh *et al.* (2015) report that *T. ludeni* and *T. urticae* eggs do not hatch at the constant temperature of 40ºC, and Roy *et al.* (2002) show that *T. mcdanieli* McGregor eggs fail to hatch at ≥ 36ºC. These findings suggest that many *Tetranychus* species may not be able to survive in regions with a period of late 30ºC to early 40ºC in a year, and that air temperature of ca. 40ºC can kill spider mite eggs for postharvest disinfestation.

We show that almost 100% of eggs hatched at 15~21 and 22~28ºC while only about 70% of eggs hatched at 29~35ºC ($F_{2,57}$ = 69.32, P < 0.0001) (Figure 2A). Among hatched mites, about 75% developed to adults under 22~28ºC compared to about 60% and 10% at 15~21ºC and 29~35ºC, respectively ($F_{2,57}$ = 224.32, P < 0.0001) (Figure 2B). These findings show that 22~28ºC is the optimal thermal condition for survival and development of *T. ludeni*. Based on the results, we propose that this mite may not be able to establish in regions or greenhouses with the daytime temperature ≥ 35ºC. The relatively low survival of immature stages at 15~21ºC may be attributed to significantly longer development period ($F_{2,1413}$ = 2328.85, P < 0.0001) (Figure 2C), which may pose higher risk of death (Murphy *et al.* 2018; Esbjerg & Sigsgaard 2019).

Like many haplodiploid species (Roy *et al.* 2003; Macke *et al.* 2011; Tamura & Ito 2017; Zhou *et al.* 2018), *T. ludeni* generally had a female-biased sex ratio (Figure 2D). However, the proportion of female offspring was significantly higher at 29~35ºC than at 15~21 and 22~28ºC ($F_{2,52}$ = 22.70, P < 0.0001) (Figure 2D). Roy *et al.* (2003) suggest that an increasing female-biased sex ratio in *T. mcdanieli* at extremely high temperatures could be an evolutionary response of spider mites to deteriorating habitats because females have better capacities than males to disperse and survive under harsh conditions.

Adult *T. ludeni* developed from 29~35ºC were significantly smaller ($F_{2,78}$ = 3.6, P = 0.0320 for male; $F_{2,106}$ = 149.54, P < 0.0001 for female) (Figure 2E) and laid significantly fewer eggs ($F_{2,37}$ = 7.88, P = 0.0014) (Figure 2F) than those from 15~21 and 22~28ºC. The present study supports both theoretical and empirical findings in many organisms, i.e. adult body size decreases with increasing temperature (Atkinson 1994; Walters & Hassall 2006; Klok & Harrison 2013) and female body size and fecundity are positively correlated (Honěk 1993). Furthermore, we demonstrate that adult longevity and temperature were inversely related in both sexes (x_2^2 = 21.53, P < 0.0001 for males; x_2^2 = 12.00, P = 0.0025 for females) with females being more tolerant than males at high temperatures (x_1^2 = 26.76, P < 0.0001 for 29~35ºC) but not at lower temperatures (x_1^2 = 1.91 and 0.01 for 15~21 and 22~28ºC, respectively; P > 0.05) (Figure 3).
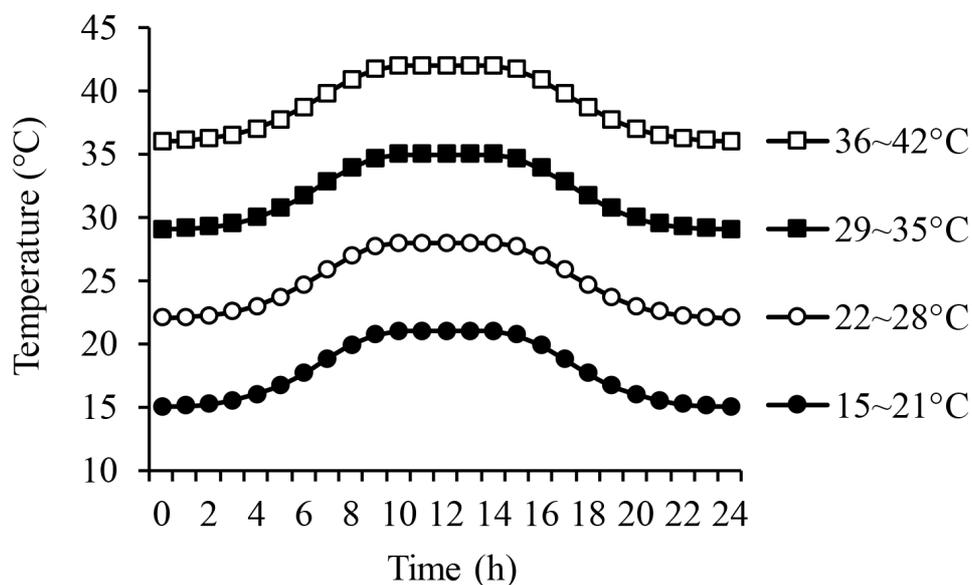
FIGURE 1. Illustration of the hourly temperature change following a modified Gaussian function (Schou *et al.* 2014):

Temperature $_{(time)}$ = $a \times e^{-[\frac{(time-b)^2}{2c^2}]}$ + d, where a (= 6) is the amplitude, b (= 10 ~ 14) is the time of the peak, c (= 3.16) is the width of the distribution, and d is the nighttime temperature. Time: 0 ~ 4 dark, 4 ~ 20 light, and 20 ~ 24 dark.
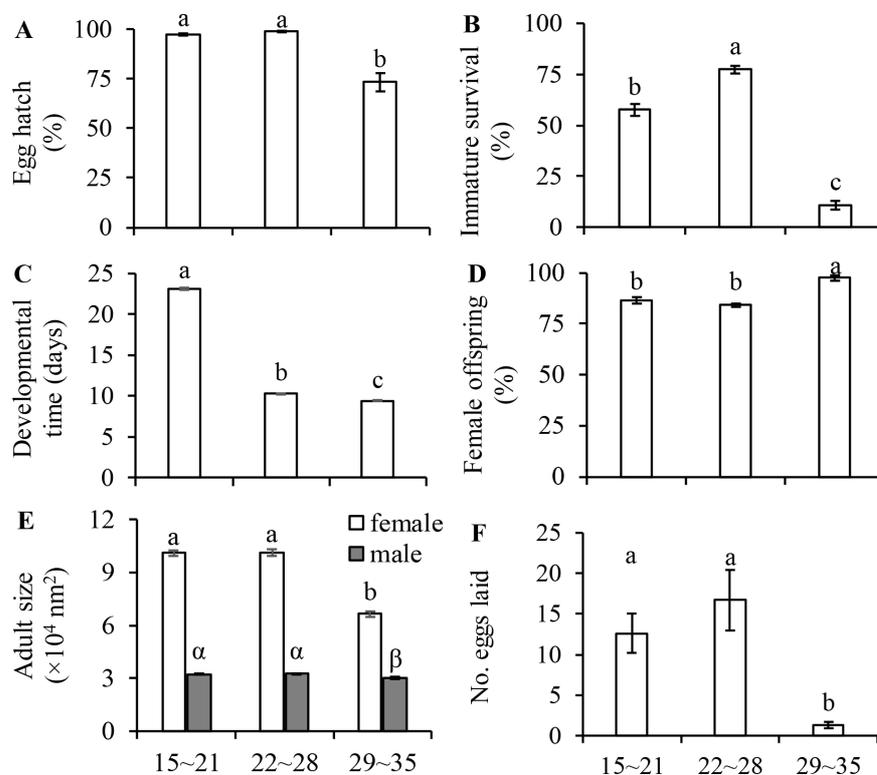

FIGURE 2. Mean (± SE) egg hatch rate (**A**), immature survival rate (**B**), developmental time (**C**), proportion of female offspring (**D**), adult size (**E**), and number of eggs laid (**F**) at different temperature ranges (ºC). For each category, columns with the same letters are not significantly different (P > 0.05).

In summary, *T. ludeni* performs the best at 22~28ºC and the worst at 29~35ºC with no eggs surviving at 36~42ºC, suggesting that this mite is less likely to invade hot to very hot regions. The mite can reproduce well at 15~21ºC but at this temperature range, it develops twice slower and suffers 25% higher immature stage mortality than at 22~28ºC, implying that this mite has some difficulty to establish in cool regions and even if it survives in these regions, it is less likely to become a major pest. Our results also suggest that *T. ludeni* can establish in the regions with mild to warm climate after invasion and become an important pest. New Zealand has a mild climate with the South Island being cooler. As a result, the mite population size may be larger in the North Island than in the South Island. Furthermore, it may not be able to survive in the regions with hot climate and greenhouses with a daytime temperature over 30ºC during the summer.
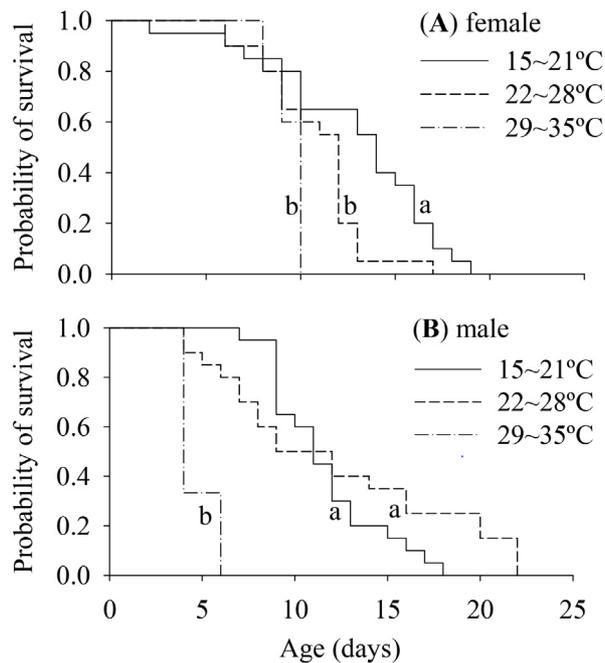

FIGURE 3. Survival of female (**A**) and male adults (**B**) at different fluctuating temperatures. Lines with the same letters are not significantly different (P > 0.05).

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