

Effects of heat stress on copulation, fecundity and longevity of newly-emerged adults of the predatory mite, *Neoseiulus barkeri* (Acari: Phytoseiidae)

Authors: Zhang, Guo-Hao, Li, Ya-Ying, Zhang, Kai-Jun, Wang, Jin-Jun, Liu, Yi-Qing, et al.

Source: Systematic and Applied Acarology, 21(3) : 295-306

Published By: Systematic and Applied Acarology Society

URL: <https://doi.org/10.11158/saa.21.3.5>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Article

Effects of heat stress on copulation, fecundity and longevity of newly-emerged adults of the predatory mite, *Neoseiulus barkeri* (Acari: Phytoseiidae)

GUO-HAO ZHANG¹, YA-YING LI¹, KAI-JUN ZHANG¹, JIN-JUN WANG¹, YI-QING LIU² & HUAI LIU^{1*}

¹ Key Laboratory of Entomology and Pest Control Engineering, College of Plant Protection, Southwest University, Chongqing 400715, People's Republic of China

² Collaborative Innovation Center of Special Plant Industry, Chongqing University of Arts and Sciences, Chongqing 402160, People's Republic of China

* Corresponding Author: liuhuai@swu.edu.cn

Abstract

Climate change predictions depict scenarios where arthropods will be more intensely and frequently exposed to extreme high temperatures. A short period of heat stress is unlikely to cause directly mortality but may modify population dynamics via impacting life history traits. In this study, the newly-emerged female and male adults of the predatory mite, *Neoseiulus barkeri* Hughes (Acari: Phytoseiidae) were exposed to 42 °C for 4 hours to investigate the heat effects on the copulation, longevity, fecundity and egg hatchability through parental effects of the mite. The results showed that after heat stress, the females had a markedly extended pre-oviposition period, shortened oviposition period, and reduced fecundity and longevity. At the meantime, when females mated with the heat stressed males, the pre-oviposition period was prolonged, the oviposition period was shortened and the fecundity was reduced. A sex-specific effect of short term heat exposure on mating behavior was further observed in males where copulation duration of the stressed individuals were somewhat prolonged. In addition, a trade-off between survival and reproduction was observed in heat stressed females. However, heat stress had no effects on immediate mortality, pre-copulation period, post-oviposition period, male longevity and egg hatchability of the progeny generations. Our results confirmed that heat stress had a detrimental effect on reproduction, particularly by delaying the onset of oviposition and reducing reproductive output and thereby influencing the population dynamics of *N. barkeri*.

Key words: *Neoseiulus barkeri*, heat stress, mating behavior, fecundity, longevity

Introduction

Phytoseiid mites (Acari: Phytoseiidae) are effective natural enemies of many phytophagous mites including *Panonychus citri* and *Tetranychus urticae* (Helle and Sabelis 1985; McMurtry and Croft 1997; McMurtry *et al.* 2013). As ectotherms, their body temperature is highly depend on ambient temperature. Previous studies had demonstrated that ambient temperature had significant impacts on predatory mites performance (e.g. functional response, mating, and oviposition behaviour), and ultimately fitness (e.g. developmental rate, lifespan, and fecundity) (Skirvin and Fenlon 2003; Nguyen and Amano 2009; Jafari *et al.* 2010; Jafari *et al.* 2012a; Xia *et al.* 2012; Wang *et al.* 2014). Currently, most thermal-related researches on predatory mites was typically conducted at a variety of constant temperatures, but seldom focused on a certain heat stress event. At extreme high temperatures, biological performance of the arthropod might be inhibited, and further sustained exposure can result in damage and injury that may eventually lead to death (Mironidis and Savopoulou-Soultani 2010; Roux *et al.* 2010; Liao *et al.* 2014).

It has been reported that heat stress for short term, i.e. several hours, can reduce longevity and fecundity of mites including *Neoseiulus californicus* (Yuan *et al.* 2015), *P. citri* (Yang *et al.* 2014), and *Mononychellus mcgregori* (Lu *et al.* 2014). Heat stress experienced at parental generation in certain species can decrease egg hatchability in their offspring generation *T. turkestanii* and *T. truncatus* (Yang *et al.* 2013), *T. viennensis* (Li *et al.* 2010), *M. mcgregori* (Lu *et al.* 2014), and *Plutella xylostella* (Zhang *et al.* 2013). Heat stress can suppress mating success in some insect species, *Aphidius colemani* (Jerbi-Elayed *et al.* 2015) and *Cnaphalocrocis medinalis* (Liao *et al.* 2014), and also can extend pre-copulation period in *P. xylostella* (Zhang *et al.* 2013). Other studies suggested that high temperature exposure have a positive effect on longevity and fecundity in *Drosophila* species (Hercus *et al.* 2003; Scannapieco *et al.* 2007), as well as in spider mite *T. viennensis* (Li *et al.* 2010). Moreover, sex-specific effects of heat stress on fecundity, viability and the developmental rates were also reported in several arthropods (Roux *et al.* 2010; Janowitz and Fischer 2011; Zhang *et al.* 2013). Females were found to be less sensitive to heat stress than males (Roux *et al.* 2010), due to the differential genes expression of heat shock proteins in females (Sørensen *et al.* 2007; Chen *et al.* 2015). Therefore, heat stress is critical for reproductive fitness and affects population dynamics via impacting life history traits.

Neoseiulus barkeri Hughes (Acari: Phytoseiidae), a generalist predator that feeds on spider mites (Fan and Pettitt 1994a; Jafari *et al.* 2010), broad mites (Fan and Pettitt 1994b), storage mites (Xia *et al.* 2012; Li *et al.* 2015), small arthropods and pollens (Bakker and Sabelis 1989; Nomikou *et al.* 2001; Wu *et al.* 2015), is considered as a good biological control agent and has been widely applied in citrus orchards targeting on citrus red mites *P. citri* (Wu *et al.* 1997; Xu and Wang 2007). It has been reported that the optimal temperature for *N. barkeri* development was estimated at 24.5 °C (Jafari *et al.* 2012b), and this mite could develop successfully and propagate with a high fecundity rate over a broad range temperatures of 24–32 °C (Xia *et al.* 2012). For most citrus growing areas, summer temperature may reach 40 °C or even higher and last for a few hours. Such scenarios may affect their population dynamics and generate failures in biological control of spider mites (Montserrat *et al.* 2013a, b). Moreover, the frequency and magnitude of extreme heat event will increase with global warming (IPCC 2014), which increase the exposure of arthropods to heat events and therefore modifying population dynamics by impacting life history traits (Li *et al.* 2010; Roux *et al.* 2010; Liang *et al.* 2014; Yang *et al.* 2014; Yuan *et al.* 2015). However, there are only a few literatures that focus on short period of heat stress on mating behavior and the subsequent reproduction of *N. barkeri* or even in other Phytoseiid mites.

Therefore, we considered the following questions in this study: (1) how a short period of heat stress imposed on virgin adults affected their performance; (2) whether any effects were sex-specific, and (3) whether effects were carried over through the egg stage, resulting in parental effects. To answer these questions, we investigated the effects of a single heat stress at 42 °C for 4 h exposure on different aspects of adult performance: mating behavior, longevity, fecundity and egg hatchability through parental effects.

Materials and methods

Test mites

The stock culture of *N. barkeri* was purchased in 2010 from the Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing, China. *N. barkeri* were fed with the flour mite, *Aleuroglyphus ovatus* on wheat bran in a 4 L translucent plastic boxes and placed in a climate-controlled room at 25 ± 1°C, 70–80 % RH, and a L:D = 14:10 photoperiod. The even-aged eggs (within 12 h) from the stock cultures were individually transferred onto a cowpea leaf arenas (2 cm

in diameter; infected with the all stages of *T. urticae* at least for 3 days). The leaf arena was floating on a piece of round sponge (4.5 cm in diameter, and 0.5 cm in thick) and absorbent cotton (4 cm in diameter) that was soaked with distilled water in a Petri dish (5 cm in diameter). The sponges and absorbent cottons were kept soaked by daily addition of distilled water, and the leaf arenas were replaced every 4–5 days. The immature stages were maintained at 25 ± 1 °C, 70–80 % RH, and L14:D10 photoperiod in a programmable temperature controller (Ningbo Southeast Instrument Co. Ltd., RDN-300B-4, China). The males and females of the newly-emerged adults (1–2 days old) were separated using a stereoscopic microscope and used for the following experiments.

Heat stress

Virgin female and male adults of *N. barkeri* were arbitrarily picked up from the culture and divided into two groups: one group was maintained at 25 °C and served as control, while the second group was stressed at 42 °C for 4 hours (heat stress treatment) and then placed back at 25 °C. The survival of the treated mite was checked immediately after heat stress, and each surviving mite was engaged in a single mating. To evaluate the heat stress on mating behavior, fecundity and longevity of females and males of *N. barkeri*, the mite from the two groups were mated in four cross experiments: (1) females and males both from control group (25♀/25♂); (2) females from the heat stress treatment group and males from control group (42♀/25♂); (3) females from the control group and males from the heat stress treatment group (25♀/42♂); (4) females and males both from the heat stress treatment group (42♀/42♂). Each experiment consisted of sixty pairs. Every 5, 10 or 20 minutes, we used a stereoscopic microscope to observe copulation duration for each mating pair placed on a leaf arena (2 cm in diameter; without prey) in a Petri dish. Observations ended at pair separation. After completion of copulation, female and male was separately transferred to leaf arenas (with abundant *T. urticae* as prey) and maintained at 25 °C for further investigations. Newly produced eggs were recorded daily and transferred onto another leaf arena to investigate egg hatchability. The surviving mites were monitored daily until female and male mite death in each experiment. Mites that escaped from the leaf arenas were excluded from the experiments.

Statistical analysis

The Kaplan-Meier method was used to analyze the survival curves of heat stressed females and males followed by log rank (Mantel-Cox) test (Lambrechts *et al.* 2011). Pre-copulation duration, copulation duration, pre-oviposition period, oviposition period, post-oviposition period, fecundity, longevity and arcsine square root transformed egg hatching rate among four paired groups were analyzed by one-way ANOVA (followed by *LSD post-hoc* tests, $P < 0.05$). In addition, to separate the effects of heat stress and the sexes on traits, two-way ANOVAs followed by *LSD post-hoc* tests were used with female and male temperature treatments as fixed factors. These analyses were performed with SPSS software (IBM SPSS Statistics 21, IBM Corporation, Somers, NY, USA).

Results

Mating behavior

Heat stress at 42 °C for 4 hours did not have an obvious effect on the pre-copulation period of *N. barkeri* (Tables 1, 2; $F_{(3, 232)} = 0.382$, $P = 0.776$), but resulted in a significantly prolonged copulation period (Tables 1, 2; $F_{(3, 232)} = 10.153$, $P < 0.001$). When control females (25♀) or heat stressed females (42♀) mated with the heat stressed males (42♂), copulation durations were extended by around 33 and 42 minutes in comparison to pairs with the males from the control groups (25♂) (Table 1).

TABLE 1. Effects of heat stress (42 °C, 4 h) on mating behavior of virgin females and males of *Neoseiulus barkeri*; results in the format: Mean ± SE.

Heat treatments (Temp. ♀/Temp. ♂)	Pre-copulation period (min)	Copulation period (min)
25♀/25♂ (N = 60)	19.67 ± 2.41 a ¹	293.33 ± 6.09 a
42♀/25♂ (N = 58)	19.14 ± 2.13 a	290.34 ± 8.58 a
25♀/42♂ (N = 59)	22.12 ± 2.39 a	326.58 ± 7.26 b
42♀/42♂ (N = 59)	21.10 ± 1.79 a	332.29 ± 5.09 b

¹Different letters in a column denote significant difference ($P < 0.05$).

TABLE 2. Results of general linear models testing the effects of female and male temperature (25 °C versus 42 °C) on reproductive traits of *Neoseiulus barkeri*.

Source	df	F	P
Pre-mating period (min)			
Female Temp.	1	0.124	0.725
Male Temp.	1	1.013	0.315
Female × male Temp.	1	0.012	0.911
Error	232		
Mating duration (min)			
Female Temp.	1	0.039	0.843
Male Temp.	1	30.054	< 0.001
Female × Male Temp.	1	0.402	0.526
Error	232		
Pre-oviposition period (d)			
Female Temp.	1	112.679	< 0.001
Male Temp.	1	139.566	< 0.001
Female × Male Temp.	1	32.383	< 0.001
Error	69		
Oviposition period (d)			
Female Temp.	1	13.181	0.001
Male Temp.	1	21.296	< 0.001
Female × Male Temp.	1	3.575	0.063
Error	69		
Post oviposition period (d)			
Female Temp.	1	2.172	0.145
Male Temp.	1	1.763	0.189
Female × Male Temp.	1	0.348	0.557
Error	69		
Female longevity (d)			
Female Temp.	1	3.353	0.071
Male Temp.	1	0.019	0.890
Female × Male Temp.	1	5.688	0.020
Error	69		

..... continued on the next page

TABLE 2 (continued)

Source	df	F	P
Fecundity (eggs/female)			
Female Temp.	1	24.526	< 0.001
Male Temp.	1	45.158	< 0.001
Female × Male Temp.	1	1.597	0.211
Error	69		
Male longevity (d)			
Female Temp.	1	0.171	0.681
Male Temp.	1	4.333	0.041
Female × Male Temp.	1	0.012	0.911
Error	72		
Egg hatchability			
Female Temp.	1	0.160	0.690
Male Temp.	1	0.488	0.486
Female × Male Temp.	1	0.031	0.861
Error	115		

Periods of pre-oviposition, oviposition and post-oviposition

The pre-oviposition periods of *N. barkeri* were significantly prolonged by heat stress for a short term (Tables 2, 3). When the heat stressed females mated with the control males (42♀/25♂), and the control females mated with the heat stressed males (25♀/42♂), their pre-oviposition period were considerably extended to 1.37 and 1.71 days in comparison to control group (25♀/25♂) (Table 3; $F_{(3, 69)} = 92.644$, $P < 0.001$). There was a synergistic effect on this trait when two sexes were stressed to heat stress (42♀/42♂), with a significant extension of 6.26 days (Tables 2, 3).

TABLE 3. Effects of heat stress on reproduction of *Neoseiulus barkeri*.

	Treatment temperatures in two sexes (Temp.♀/Temp.♂)			
	25♀/25♂	42♀/25♂	25♀/42♂	42♀/42♂
Pre-oviposition period (d)	4.45 ± 0.14 a ¹	5.82 ± 0.26 b	6.16 ± 0.30 b	10.71 ± 0.39 c
Oviposition period (d)	27.20 ± 0.67 b	21.00 ± 1.70 a	19.89 ± 0.84 a	17.94 ± 1.19 a
Post-oviposition period (d)	23.35 ± 1.33 a	20.06 ± 1.45 a	24.52 ± 1.56 a	23.12 ± 2.02 a
Fecundity (eggs/female)	35.55 ± 0.76 c	28.65 ± 0.90 b	26.68 ± 1.11 b	22.59 ± 1.59 a
Female longevity (d)	54.45 ± 1.57 b	46.29 ± 2.08 a	50.11 ± 1.74 ab	51.18 ± 2.38 ab
Male longevity (d)	58.37 ± 1.55 a	57.35 ± 1.98 a	54.11 ± 1.84 a	53.53 ± 2.30 a
Egg hatchability (%)	97.25 ± 0.91 a	96.72 ± 1.66 a	96.39 ± 1.37 a	96.72 ± 0.99 a

¹Different letters in a row denote significant difference ($P < 0.05$).

The oviposition period in the heat stressed pairs tended to be shorter when heat stressed only in female (42♀/25♂, 21.00 days) or male (25♀/42♂, 19.89 days), or both (42♀/42♂, 17.94 days) than in the control pairs (25♀/25♂, 27.20 days) (Table 2, 3; $F_{(3, 69)} = 13.327$, $P < 0.001$). There was also a synergistic effect on this trait when two sexes were stressed to heat stress. However, post-oviposition period among treatments was not affected by heat stress (Table 2, 3; $F_{(3, 69)} = 1.386$, $P = 0.254$).

Fecundity, longevity and egg hatchability

Females in control group (25♀/25♂) had the highest fecundity (35.55 ± 0.76 eggs/female), followed by treatments involving heat stress only on females (42♀/25♂: 28.65 ± 0.90 eggs/female), then males (25♀/42♂: 26.68 ± 1.11 eggs/female), and then both (42♀/42♂: 22.59 ± 1.59 eggs/female) (Tables 2, 3; $F_{(3, 69)} = 24.565$, $P < 0.001$). However, egg hatchability was not affected by heat stress (Tables 2, 3; $F_{(3, 115)} = 0.230$, $P = 0.875$), with an average of 96.78 ± 0.61 % eggs hatched successfully.

Females had a shorter longevity than males ($F_{(1, 147)} = 13.856$, $P < 0.001$), with mean (\pm SE) longevity across all treatment groups being 50.66 ± 1.01 days for females and 55.88 ± 0.98 days for males. When stressed at 42 °C for 4 hours, female mites (42♀/25♂) had a 14.99 % decreased longevity in comparison with the control group (Table 3; $F_{(3, 70)} = 3.050$, $P = 0.034$). On the other hand, there was no significant effect of heat stress on male longevity (Table 3; $F_{(3, 72)} = 1.503$, $P = 0.221$).

The age-specific survival of female l_x (percentage of surviving females at the instant x) and age-specific fecundity rate m_x (number of eggs laid per female per day), and the age-specific survival of male l_x (percentage of surviving males at the instant x) of *N. barkeri* from the four cross combinations stressed at 42 °C for 4 h are shown in Figure 1 and 2, respectively. Survival curves of females were significantly different (Figure 1) according to log-rank tests (overall: $\chi^2 = 8.394$, $df = 3$, $P = 0.039$; 25♀/25♂ vs. 42♀/25♂: $P = 0.013$; 25♀/25♂ vs. 25♀/42♂: $P = 0.040$; 25♀/25♂ vs. 42♀/42♂: $P = 0.495$; 42♀/25♂ vs. 25♀/42♂: $P = 0.273$; 42♀/25♂ vs. 42♀/42♂: $P = 0.084$; 25♀/42♂ vs. 42♀/42♂: $P = 0.246$). On the contrary, survival curves of males did not differ significantly from one another (overall: $\chi^2 = 3.860$, $df = 3$, $P = 0.277$) (Figure 2).

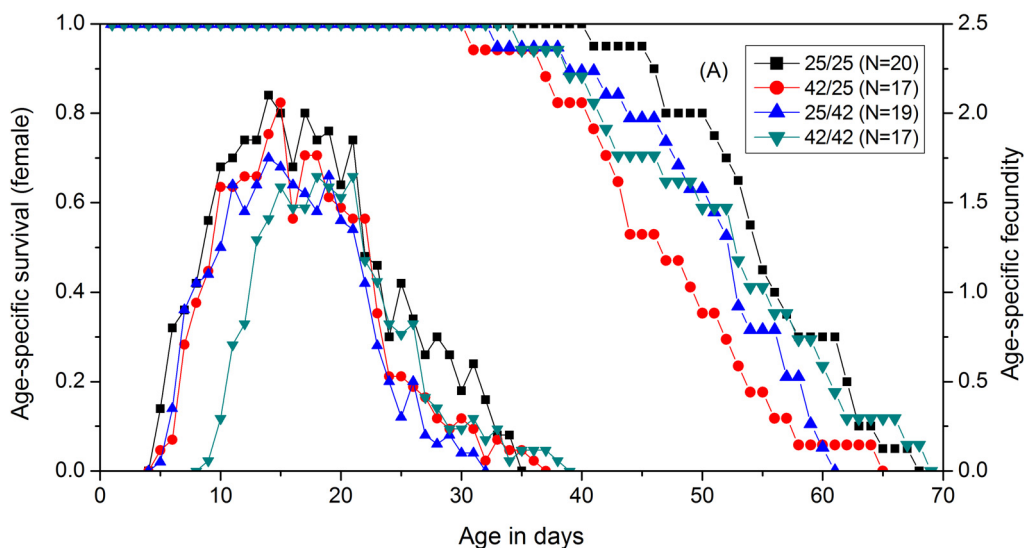


FIGURE 1. Effect of heat stress on the age-specific survival rate (l_x) and age-specific fecundity (m_x) in female adult of *N. barkeri*. Treatments involved different combinations of female and male exposure to 42 °C for 4 h. 25♀/25♂: females and males both from control group; 42♀/25♂: females from the heat stress treatment group and males from control group; 25♀/42♂: females from the control group and males from the heat stress treatment group; 42♀/42♂: females and males both from the heat stress treatment group. “N” refers to the number of individuals.

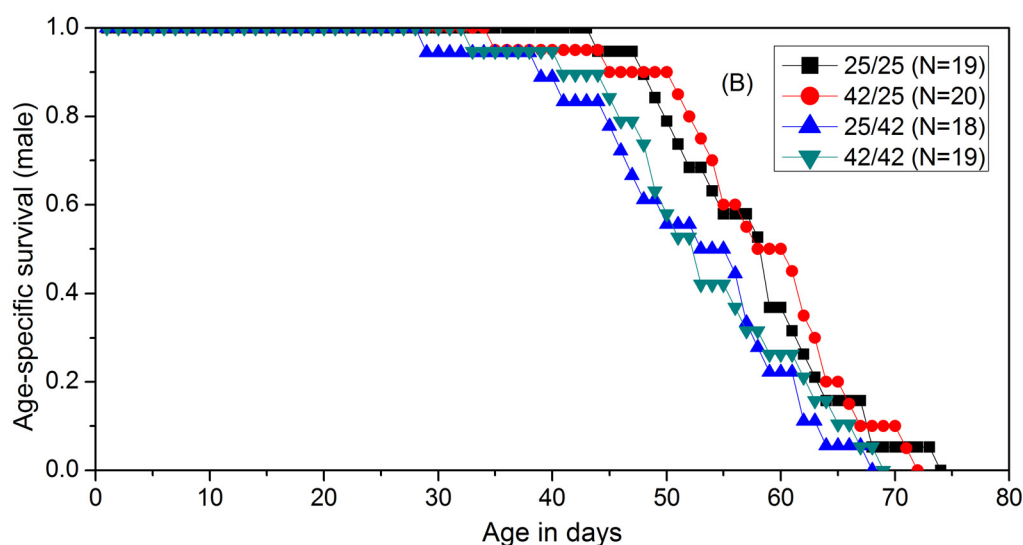


FIGURE 2. Effect of heat stress on the age-specific survival rate (l_x) in male adult of *N. barkeri*. Treatments were the same as Figure 1.

Discussion

This study investigated the impacts of a single extreme heat event (42 °C, 4 h) on the performance of newly-emerged adults of *N. barkeri* as well as the consequences for egg hatchability in progeny generation. Adult stage was tested in this study because heat stress experienced at which might cause greater detrimental effects on reproduction than other developmental stages (Li *et al.* 2010; Zhang *et al.* 2015).

Mating and egg laying behavior in *N. barkeri* begin only after the copulation, and females require multiple mating to produce the maximum fecundity (Momen 1993; Pappas *et al.* 2007; Gotoh and Tsuchiya 2008). Males recognize females by direct contact and show an initiative behavior in copulation (Pappas *et al.* 2005). No difference in pre-copulation duration among different treatments indicated that the mobility of the heat stressed *N. barkeri* was not affected by short term heat stress. Previous study reported that copulation duration of *N. barkeri* was on average of 285 minutes at 27–29 °C (Momen 1993), which was a little shorter than our result of 293 minutes at 25 °C. The difference may be partly a result of different ambient temperature for the reason that temperature at the time of mating strictly determined copulation duration (Nguyen and Amano 2010). In addition, the sex-specific extended copulation duration in heat stressed males indicated that spermatophore transfer rate might be transiently inhibited after heat stress (Liao *et al.* 2014).

The prolonged pre-oviposition period, reduced oviposition period, longevity and total fecundity in heat stressed female adults suggested that heat stress could reduce their longevity and fecundity (Yang *et al.* 2014; Yuan *et al.* 2015). However, our result was different from the unaffected or even increased fecundity in heat stressed *T. turkestani* (Yang *et al.* 2013) and *T. viennensis* (Li *et al.* 2010). We concluded that the different heat shock response might be one of the reasons for outbreaks of some *Tetranychus* mites under hot and dry conditions (Montserrat *et al.* 2013a). On the other hand, heat stress also had negative effects on male fertility rather than longevity. Our study clearly indicated that the survival curves females were significantly affected by heat stress, especially when 25♀/25♂ vs. 42♀/42♂, which suggested that there might be a trade-off between longevity and reproduction (Speakman and Garratt 2014; Travers *et al.* 2015). Considering the longer longevity

observed in males and the significant reduced longevity observed in heat stressed female adults in this study, we considered that female mites were more sensitive to heat stress than male mites on a life span scale, which is different the result of previous study in insects or mites (Sørensen *et al.* 2007; Roux *et al.* 2010; Chen *et al.* 2015).

The reduced fitness after heat stress could be attributed to several different aspects, including direct mortality and damage (Mironidis and Savopoulou-Soultani 2010; Liao *et al.* 2014), inhibition of prey consumption (unpublished data), male fertility (David *et al.* 2005; Nguyen *et al.* 2013; Chirault *et al.* 2015), as well as oxidative stress (Yang *et al.* 2010; Lu *et al.* 2014; Zhang *et al.* 2014). Chirault *et al.* (2015) reported that heat stress could cause a delay in spermatogenesis during development and a significant decrease in sperm stock at male adult emergence. In this study, the process of oogenesis and spermatogenesis in heat stressed *N. barkeri* must have been complete, because each tested individual had capacity to lay eggs and almost all eggs hatched successfully. Therefore, spermatophores and oocytes were most likely to be damaged, which might cause a significantly reduced fecundity, especially when females and males were stressed together. However, there is no powerful evidence that could testify this hypothesis, which needs further investigations. Previous studies indicated that the quantity of spermatophores and/or seminal fluids transferred by males could reduce female egg production in some insect species (Katsuki and Miyatake 2009; Chirault *et al.* 2015). Although reduced fecundity were observed, there was no negative impact on egg hatchability via a parental effect manner that had reported in some other mites or insects (Li *et al.* 2010; Yang *et al.* 2013; Zhang *et al.* 2013; Liang *et al.* 2014).

We confirmed that such a short term heat stress did have negative effects on the performance of *N. barkeri*. Female adults were more susceptible to heat stress than male adults owing to the significantly reduced fitness in fecundity and longevity. Heat stress had no impact on male longevity or on the later repercussions for their progeny. Biological control of pest mites in orchards and greenhouses using phytoseiid mites has been considered as a key strategy for the integrated pest management program (Niu *et al.* 2014; Zalucki *et al.* 2015). However, many studies have indicated that natural enemies have lower tolerance to higher temperature than their prey (Roy *et al.* 2003; Stavriniades *et al.* 2010; Ozawa *et al.* 2012; Coombs and Bale 2013; Montserrat *et al.* 2013b). High temperature is usually accompanied with low air humidity. Hot and dry weather create favorable condition for the seasonal outbreaks of pest mites in orchards, but demote predatory mite abundance, which might cause a direct disruption of biological control in agro-ecosystems (Montserrat *et al.* 2013a). Therefore, more immediate actions should be taken to enhance biological control efficiency such as selecting low humidity and high temperature resistant strains of phytoseiid mites.

Acknowledgements

We thank two anonymous referees for their helpful comments and suggestions on the manuscript. This study was supported by the Fundamental Research Funds for the Central Universities (XDJK2015D018, XDJK2014C097), National Public Benefit Industry (Agriculture) Research Projects, the Ministry of Agriculture, (200903032) and Chongqing Postdoctoral Science special Foundation (Xm2014047).

References

- Bakker, F. & Sabelis, M. (1989) How larvae of *Thrips tabaci* reduce the attack success of phytoseiid predators. *Entomologia Experimentalis et Applicata*, 50(1), 47–51.

- <http://dx.doi.org/10.1111/j.1570-7458.1989.tb02313.x>
- Chen, W., Li, D.S., Zhang, M., Zhao, Y.L., Wu, W.J. & Zhang, G.R. (2015) Cloning and differential expression of five heat shock protein genes associated with thermal stress and development in the polyphagous predatory mite *Neoseiulus cucumeris* (Acari: Phytoseiidae). *Experimental and Applied Acarology*, 67(1), 65–85.
- <http://dx.doi.org/10.1007/s10493-015-9933-0>
- Chirault, M., Lucas, C., Goubault, M., Chevrier, C., Bressac, C., Lecureuil, C., 2015. A combined approach to heat stress effect on male fertility in *Nasonia vitripennis*: from the physiological consequences on spermatogenesis to the reproductive adjustment of females mated with stressed males. *PLoS ONE*, 10, e0120656.
- <http://dx.doi.org/10.1371/journal.pone.0120656>
- Coombs, M.R. & Bale, J.S. (2013) Comparison of thermal activity thresholds of the spider mite predators *Phytoseiulus macropilis* and *Phytoseiulus persimilis* (Acari: Phytoseiidae). *Experimental and Applied Acarology*, 59(4), 435–445.
- <http://dx.doi.org/10.1007/s10493-012-9619-9>
- David, J.R., Araripe, L.O., Chakir, M., Legout, H., Lemos, B., Petavy, G., Rohmer, C., Joly, D. & Moreteau, B. (2005) Male sterility at extreme temperatures: a significant but neglected phenomenon for understanding *Drosophila* climatic adaptations. *Journal of Evolutionary Biology*, 18(4), 838–846.
- <http://dx.doi.org/10.1111/j.1420-9101.2005.00914.x>
- Fan, Y.Q. & Pettitt, F.L. (1994a) Biological control of broad mite, *Polyphagotarsonemus latus* (Banks), by *Neoseiulus barkeri* Hughes on pepper. *Biological Control*, 4(4), 390–395.
- <http://dx.doi.org/10.1006/bcon.1994.1049>
- Fan, Y.Q. & Pettitt, F.L. (1994b) Functional response of *Neoseiulus barkeri* Hughes on two-spotted spider mite (Acari: Tetranychidae). *Experimental and Applied Acarology*, 18(10), 613–621.
- <http://dx.doi.org/10.1007/BF00051724>
- Gotoh, T. & Tsuchiya, A. (2008) Effect of multiple mating on reproduction and longevity of the phytoseiid mite *Neoseiulus californicus*. *Experimental and Applied Acarology*, 44(3), 185–197.
- <http://dx.doi.org/10.1007/s10493-008-9143-0>
- Helle, W. & Sabelis, M.W. (1985) Spider mites: Their biology, natural enemies, and control. Amsterdam, Elsevier.
- Hercus, M.J., Loeschcke, V. & Rattan, S.I.S. (2003) Lifespan extension of *Drosophila melanogaster* through hormesis by repeated mild heat stress. *Biogerontology*, 4(3), 149–156.
- <http://dx.doi.org/10.1023/a:1024197806855>
- IPCC (2014) Climate change 2014: Synthesis report. Contribution of working groups i, ii and iii to the fifth assessment report of the intergovernmental panel on climate change [core writing team, r.K. Pachauri and l.A. Meyer (eds.)]. Ipcc, geneva, switzerland, 151 pp.
- Jafari, S., Fathipour, Y. & Faraji, F. (2012a) The influence of temperature on the functional response and prey consumption of *Neoseiulus barkeri* (Acari: Phytoseiidae) on *Tetranychus urticae* (Acari: Tetranychidae). *Journal of Entomological Society of Iran*, 31(2), 39–52.
- Jafari, S., Fathipour, Y. & Faraji, F. (2012b) Temperature-dependent development of *Neoseiulus barkeri* (Acari: Phytoseiidae) on *Tetranychus urticae* (Acari: Tetranychidae) at seven constant temperatures. *Insect Science*, 19(2), 220–228.
- <http://dx.doi.org/10.1111/j.1744-7917.2011.01444.x>
- Jafari, S., Fathipour, Y., Faraji, F. & Bagheri, M. (2010) Demographic response to constant temperatures in *Neoseiulus barkeri* (Phytoseiidae) fed on *Tetranychus urticae* (Tetranychidae). *Systematic and Applied Acarology*, 15(2), 83–99.
- <http://dx.doi.org/10.11158/saa.15.2.1>
- Janowitz, S.A. & Fischer, K. (2011) Opposing effects of heat stress on male versus female reproductive success in *Bicyclus anynana* butterflies. *Journal of Thermal Biology*, 36(5), 283–287.
- <http://dx.doi.org/10.1016/j.jtherbio.2011.04.001>
- Jerbi-Elayed, M., Lebdi-Grissa, K., Foray, V., Muratori, F. & Hance, T. (2015) Using multiple traits to estimate the effects of heat shock on the fitness of *Aphidius colemani*. *Entomologia Experimentalis et Applicata*, 155(1), 18–27.
- <http://dx.doi.org/10.1111/eea.12273>
- Katsuki, M. & Miyatake, T. (2009) Effects of temperature on mating duration, sperm transfer and remating frequency in *Callosobruchus chinensis*. *Journal of Insect Physiology*, 55(2), 112–115.

- <http://dx.doi.org/10.1016/j.jinsphys.2008.10.012>
- Lambrechts, L., Paaijmans, K.P., Fansiri, T., Carrington, L.B., Kramer, L.D., Thomas, M.B. & Scott, T.W. (2011) Impact of daily temperature fluctuations on dengue virus transmission by *Aedes aegypti*. *Proceedings of the National Academy of Sciences of the United States of America*, 108(18), 7460–7465.
<http://dx.doi.org/10.1073/pnas.1101377108>
- Li, D.X., Zhang, X.N., Yang, Y.L. & Zhu, H.W. (2010) Effects of high temperature shocks on hawhorn spider mite, *Tetranychus viennensis* Zacher. *Acta Ecologica Sinica*, 30(16), 4437–4444 (In Chinese with English Abstract).
- Li, Y.Y., Zhang, Y., Hu, Q., Liu, L., Xu, X.N., Liu, H. & Wang, J.J. (2015) Effect of bran moisture content and initial population density on mass production of *Tyrophagus putrescentiae* (Schrank) (Acari: Acaridae). *Systematic and Applied Acarology*, 20(5), 497–506.
<http://dx.doi.org/10.11158/saa.20.5.6>
- Liang, L.N., Zhang, W., Ma, G., Hoffmann, A.A. & Ma, C.S. (2014) A single hot event stimulates adult performance but reduces egg survival in the oriental fruit moth, *Grapholitha molesta*. *PLoS ONE*, 9, e116339.
<http://dx.doi.org/10.1371/journal.pone.0116339>
- Liao, H.J., Qian, Q. & Liu, X.D. (2014) Heat shock suppresses mating and sperm transfer in the rice leaf folder *Cnaphalocrocis medinalis*. *Bulletin of Entomological Research*, 104(3), 383–392.
<http://dx.doi.org/10.1017/S0007485314000212>
- Lu, F.P., Chen, Q., Chen, Z.S., Lu, H., Xu, X.L. & Jing, F.L. (2014) Effects of heat stress on development, reproduction and activities of protective enzymes in *Mononychellus mcgregori*. *Experimental and Applied Acarology*, 63(2), 267–284.
<http://dx.doi.org/10.1007/s10493-014-9784-0>
- McMurtry, J. & Croft, B. (1997) Life styles of phytoseiid mites and their roles in biological control. *Annual Review of Entomology*, 42(1), 291–321.
<http://dx.doi.org/10.1146/annurev.ento.42.1.291>
- McMurtry, J.A., Moraes, G.J. & Sourassou, N.F. (2013) Revision of the lifestyle of phytoseiid mites (Acari: Phytoseiidae) and implications for biological control strategies. *Systematic & Applied Acarology*, 18, 297–320.
<http://dx.doi.org/10.11158/saa.18.4.1>
- Mironidis, G.K. & Savopoulou-Soultani, M. (2010) Effects of heat shock on survival and reproduction of *Helicoverpa armigera* (Lepidoptera: Noctuidae) adults. *Journal of Thermal Biology*, 35(2), 59–69.
<http://dx.doi.org/10.1016/j.jtherbio.2009.11.001>
- Momen, F.M. (1993) Effects of single and multiple copulation on fecundity, longevity and sex-ratio of the predacious mite *Amblyseius barkeri* (Hugh.) (Acari: Phytoseiidae). *Anzeiger Fur Schadlingskunde Pflanzen-schutz Umweltschutz*, 66(8), 148–150.
<http://dx.doi.org/10.1007/Bf01983026>
- Montserrat, M., Guzmán, C., Sahún, R.M., Belda, J.E. & Hormaza, J.I. (2013a) Pollen supply promotes, but high temperatures demote, predatory mite abundance in avocado orchards. *Agriculture, Ecosystems & Environment*, 164, 155–161.
<http://dx.doi.org/10.1016/j.agee.2012.09.014>
- Montserrat, M., Sahun, R.M. & Guzman, C. (2013b) Can climate change jeopardize predator control of invasive herbivore species? A case study in avocado agro-ecosystems in Spain. *Experimental and Applied Acarology*, 59(1), 27–42.
<http://dx.doi.org/10.1007/s10493-012-9560-y>
- Nguyen, T.M., Bressac, C. & Chevrier, C. (2013) Heat stress affects male reproduction in a parasitoid wasp. *Journal of Insect Physiology*, 59(3), 248–254.
<http://dx.doi.org/10.1016/j.jinsphys.2012.12.001>
- Nguyen, T.T.P. & Amano, H. (2009) Mating duration and egg production of the predaceous mite *Neoseiulus californicus* (Acari: Phytoseiidae) vary with temperature. *Journal of Asia-Pacific Entomology*, 12(4), 297–299.
<http://dx.doi.org/10.1016/j.aspen.2009.06.003>
- Nguyen, T.T.P. & Amano, H. (2010) Temperature at immature and adult stages differentially affects mating duration and egg production of *Neoseiulus californicus* females mated once (Acari: Phytoseiidae). *Journal of Asia-Pacific Entomology*, 13(1), 65–68.
<http://dx.doi.org/10.1016/j.aspen.2009.10.002>
- Niu, J.Z., Hull-Sanders, H., Zhang, Y.X., Lin, J.Z., Dou, W. & Wang, J.J. (2014) Biological control of arthro-

- pod pests in citrus orchards in China. *Biological Control*, 68, 15–22.
<http://dx.doi.org/10.1016/j.biocontrol.2013.06.005>
- Nomikou, M., Janssen, A., Schraag, R. & Sabelis, M.W. (2001) Phytoseiid predators as potential biological control agents for *Bemisia tabaci*. *Experimental and Applied Acarology* 25(4), 271–291.
<http://dx.doi.org/10.1023/a:1017976725685>
- Ozawa, R., Nishimura, O., Yazawa, S., Muroi, A., Takabayashi, J. & Arimura, G. (2012) Temperature-dependent, behavioural, and transcriptional variability of a tritrophic interaction consisting of bean, herbivorous mite, and predator. *Molecular Ecology*, 21(22), 5624–5635.
<http://dx.doi.org/10.1111/mec.12052>
- Pappas, M.L., Broufas, G.D. & Koveos, D.S. (2005) Mating behavior of the predatory mite *Kampimodromus aberrans* (Acari: Phytoseiidae). *Experimental and Applied Acarology*, 36(3), 187–197.
<http://dx.doi.org/10.1007/s10493-005-5303-7>
- Pappas, M.L., Broufas, G.D. & Koveos, D.S. (2007) Effect of mating frequency on fecundity and longevity of the predatory mite *Kampimodromus aberrans* (Acari: Phytoseiidae). *Experimental and Applied Acarology*, 43(3), 161–170.
<http://dx.doi.org/10.1007/s10493-007-9112-z>
- Roux, O., Le Lann, C., van Alphen, J.J.M. & van Baaren, J. (2010) How does heat shock affect the life history traits of adults and progeny of the aphid parasitoid *Aphidius avenae* (Hymenoptera: Aphidiidae)? *Bulletin of Entomological Research*, 100(5), 543–549.
<http://dx.doi.org/10.1017/s0007485309990575>
- Roy, M., Brodeur, J. & Cloutier, C. (2003) Effect of temperature on intrinsic rates of natural increase (r_m) of a coccinellid and its spider mite prey. *BioControl* 48(1), 57–72.
<http://dx.doi.org/10.1023/a:1021289832664>
- Scannapieco, A.C., Sorensen, J.G., Loeschcke, V. & Norry, F.M. (2007) Heat-induced hormesis in longevity of two sibling *Drosophila* species. *Biogerontology*, 8(3), 315–325.
<http://dx.doi.org/10.1007/s10522-006-9075-1>
- Skirvin, D.J. & Fenlon, J.S. (2003) The effect of temperature on the functional response of *Phytoseiulus persimilis* (Acari: Phytoseiidae). *Experimental and Applied Acarology*, 31(1), 37–49.
<http://dx.doi.org/10.1023/b:appa.0000005107.97373.87>
- Sørensen, J.G., Kristensen, T.N., Kristensen, K.V. & Loeschcke, V. (2007) Sex specific effects of heat induced hormesis in Hsf-deficient *Drosophila melanogaster*. *Experimental Gerontology*, 42(12), 1123–1129.
<http://dx.doi.org/10.1016/j.exger.2007.09.001>
- Speakman, J.R. & Garratt, M. (2014) Oxidative stress as a cost of reproduction: Beyond the simplistic trade-off model. *Bioessays*, 36(1), 93–106.
<http://dx.doi.org/10.1002/bies.201300108>
- Stavrinides, M.C., Daane, K.M., Lampinen, B.D. & Mills, N.J. (2010) Plant water stress, leaf temperature, and spider mite (Acari: Tetranychidae) outbreaks in California vineyards. *Environmental Entomology*, 39(4), 1232–1241.
<http://dx.doi.org/10.1603/EN09288>
- Travers, L.M., Garcia-Gonzalez, F. & Simmons, L.W. (2015) Live fast die young life history in females: Evolutionary trade-off between early life mating and lifespan in female *Drosophila melanogaster*. *Scientific Reports*, 5, 15469.
<http://dx.doi.org/10.1038/srep15469>
- Wang, Z.Y., Qin, S.Y., Xiao, U.F. & Liu, H. (2014) Effects of temperature on development and reproduction of *Euseius nicholsi* (Ehara & Lee). *Systematic and Applied Acarology*, 19(1), 44–50.
<http://dx.doi.org/10.11158/saa.19.1.2>
- Wu, S.Y., Gao, Y.L., Xu, X.N., Wang, D.J., Li, J., Wang, H.H., Wang, E.D. & Lei, Z.R. (2015) Feeding on *Beauveria bassiana*-treated *Frankliniella occidentalis* causes negative effects on the predatory mite *Neoseiulus barkeri*. *Scientific Reports*, 5, 12033.
<http://dx.doi.org/10.1038/srep12033>
- Wu, W.N., Liang, L.R. & Lan, W.M. (1997) *Economic insect fauna of China (Acari: Phytoseiidae)*. Beijing: Science press (In Chinese), 223 pp.
- Xia, B., Zou, Z.W., Li, P.X. & Lin, P. (2012) Effect of temperature on development and reproduction of *Neoseiulus barkeri* (Acari: Phytoseiidae) fed on *Aleuroglyphus ovatus*. *Experimental and Applied Acarology*, 56(1), 33–41.
<http://dx.doi.org/10.1007/s10493-011-9481-1>

- Xu, X.N. & Wang, E.D. (2007) Statue and analysis of oversease natural enemies merchandise. *Chinese Journal of Biological Control*, 23(4), 373–382 (In Chinese).
- Yang, L.H., Huang, H. & Wang, J.J. (2010) Antioxidant responses of citrus red mite, *Panonychus citri* (Mcgregor) (Acari: Tetranychidae), exposed to thermal stress. *Journal of Insect Physiology*, 56(12), 1871–1876.
<http://dx.doi.org/10.1016/j.jinsphys.2010.08.006>
- Yang, L.H., Huang, H. & Wang, J.J. (2014) Effect of exposure to heat stress on survival and fecundity of *Panonychus citri*. *Scientia Agricultura Sinica*, 47(4), 693–701 (In Chinese with English Abstract).
<http://dx.doi.org/10.3864/j.issn.0578-1752.2014.04.009>
- Yang, S., Zhao, B.M., Li, G.Y., Hu, S.L., Guo, Y.L. & Zhang, J.P. (2013) Effects of brief exposure to high temperature on *Tetranychus turkestanii* and *T. truncatus* (Acari: Tetranychidae). *Acta Entomologica Sinica*, 56(3), 276–285 (In Chinese with English Abstract).
- Yuan, X.P., Wang, X.D., Wang, J.W. & Zhao, Y.Y. (2015) Effects of brief exposure to high temperature on *Neoseiulus californicus*. *Chinese Journal of Applied Ecology*, 26(3), 853–858 (In Chinese with English Abstract).
<http://dx.doi.org/10.13287/j.1001-9332.20150122.002>
- Zalucki, M.P., Furlong, M.J., Schellhorn, N.A., Macfadyen, S. & Davies, A.P. (2015) Assessing the impact of natural enemies in agroecosystems: Toward “real” IPM or in quest of the Holy Grail? *Insect Science*, 22(1), 1–5.
<http://dx.doi.org/10.1111/1744-7917.12172>
- Zhang, G.H., Liu, H., Wang, J.J. & Wang, Z.Y. (2014) Effects of thermal stress on lipid peroxidation and antioxidant enzyme activities of the predatory mite, *Neoseiulus cucumeris* (Acari: Phytoseiidae). *Experimental and Applied Acarology*, 64(1), 73–85.
<http://dx.doi.org/10.1007/s10493-014-9806-y>
- Zhang, W., Chang, X.Q., Hoffmann, A., Zhang, S. & Ma, C.S. (2015) Impact of hot events at different developmental stages of a moth: the closer to adult stage, the less reproductive output. *Scientific Reports*, 5, 10436.
<http://dx.doi.org/10.1038/srep10436>
- Zhang, W., Zhao, F., Hoffmann, A.A. & Ma, C.S. (2013) A single hot event that does not affect survival but decreases reproduction in the diamondback moth, *Plutella xylostella*. *PLoS ONE*, 8(10), e75923.
<http://dx.doi.org/10.1371/journal.pone.0075923.g001>

Submitted: 26 Aug. 2015; accepted by Zhi-Qiang Zhang: 1 Dec. 2015; published: 15 Feb. 2016