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Article

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

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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 ºC 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. turkestani* 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 Petitt 1994a; Jafari *et al*. 2010), broad mites (Fan and Petitt 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 ºC (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 ºC (Xia *et al*. 2012). For most citrus growing areas, summer temperature may reach 40 ºC 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 ± 1ºC, 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 ºC, 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 ºC and served as control, while the second group was stressed at 42 ºC for 4 hours (heat stress treatment) and then placed back at 25 ºC. 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 ºC 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 ºC, 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

[1]Different 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		

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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

[1]Different 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 (± 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).

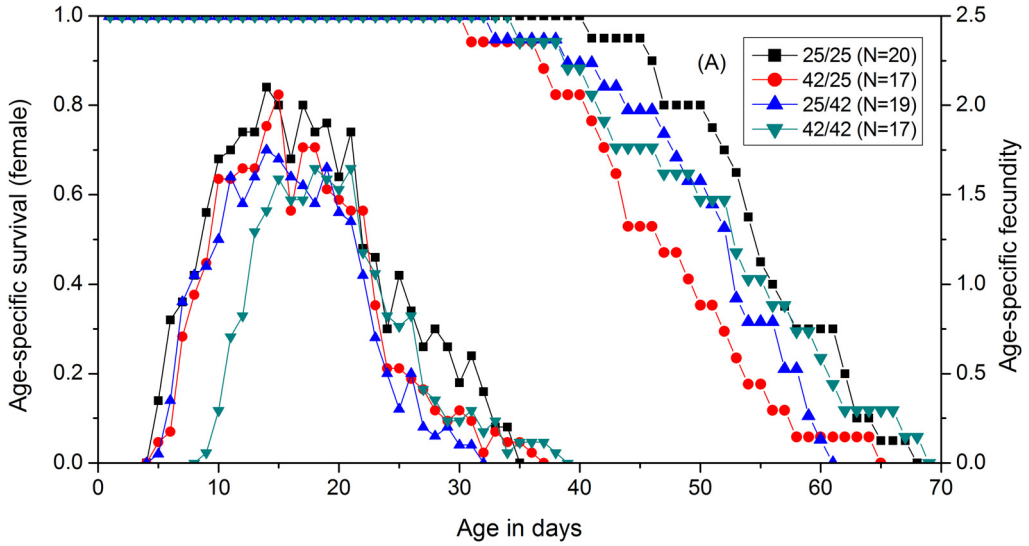

FIGURE 1. Effect of heat stress on the age-specific survival rate (l_x) and age-specific fecundity (m_x) in female adult of *N. barkeri*. Treatments involved different combinations of female and male exposure to 42 ºC for 4 h. 25♀/25♂: females and males both from control group; 42♀/25♂: females from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

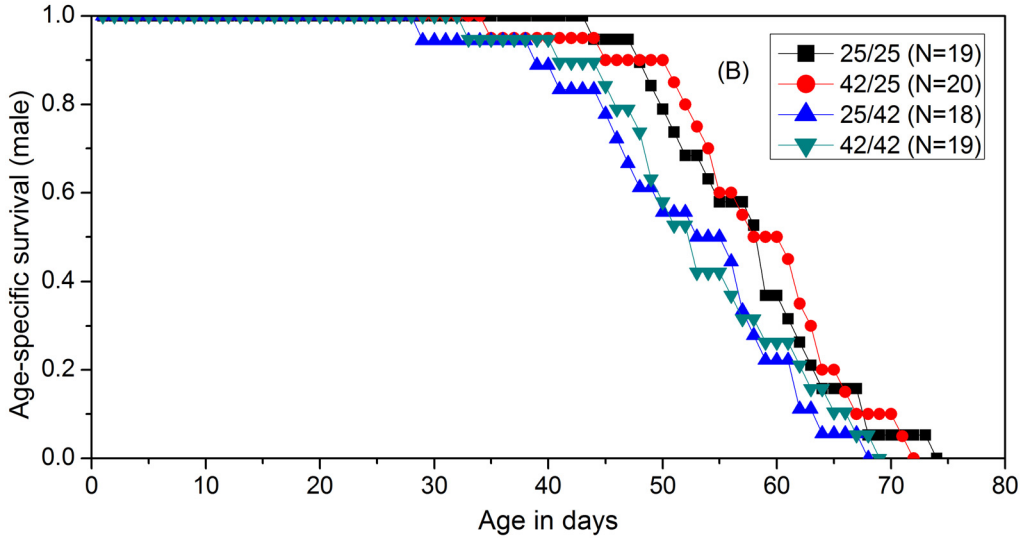

FIGURE 2. Effect of heat stress on the age-specific survival rate (l_x) in male adult of *N. barkeri*. Treatments were the same as Figure 1.

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; Stavrinides *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.

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