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ORIGINAL PAPER

Consequences of elevated temperature on the biology, predation, and competitiveness of two mirid predators in the rice ecosystem

Yueliang Bai[1,2] · Md. Khairul Quais[1,3] · Wenwu Zhou[1,2] · Zeng-Rong Zhu[1,2]

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Abstract

Temperature is an important environmental factor in agriculture, affecting individual organisms and the entire farmland ecosystem. Global warming has become more tangible, which may negatively affect pest biological control due to the generally weak thermal tolerance of natural enemies. The mirids *Cyrtorhinus lividipennis* and *Tytthus chinensis* (Insecta: Hemiptera: Miridae) are important natural predators of planthoppers and leafhoppers in Asian paddy fields. However, the effects of thermal stress on these predators remain poorly understood. We investigated the thermal tolerance, fitness, predation abilities, and transcriptomic response of *T. chinensis* and *C. lividipennis* at elevated temperatures. *T. chinensis* was more heat tolerant than both *Nilaparvata lugens* (its prey) and *C. lividipennis*. *T. chinensis* not only exhibited better development, survival, reproduction, and predation capacities compared with *C. lividipennis* but also showed stronger competitiveness when the two mirid predators co-persisted under high-temperature conditions. To understand the underlying mechanisms, we sequenced their transcriptomes at different temperatures. Heat shock protein (*HSP*) genes were identified and analyzed due to their high co-regulation during heat treatment. Quantitative polymerase chain reaction results showed that *T. chinensis* induces *HSPs* expression quickly and strongly over a wider temperature range in response to heat stress compared with *C. lividipennis*. Taken together, we highlighted the potential of *T. chinensis* as a biological control agent in future global warming conditions and provided insight into the thermal adaption of mirid species.

Keywords *Cyrtorhinus lividipennis* · *Tytthus chinensis* · Thermal tolerance · Predation efficacy · Heat shock proteins

Key Message

- *Cyrtorhinus lividipennis* and *Tytthus chinensis* are niche-overlap predators of many important pests in rice fields.
- *T. chinensis* shows greater tolerance, fitness, and predation compared with *C. lividipennis* under high-temperature conditions.
- As the temperature rises, the competitiveness of *T. chinensis* increases, while that of *C. lividipennis* decreases.
- *C. lividipennis* and *T. chinensis* show different *HSP* expression patterns after heat treatment.
- *T. chinensis* shows better potential as a biological control agent under global warming conditions.

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✉ Zeng-Rong Zhu
zrzhu@zju.edu.cn

[1] State Key Laboratory of Rice Biology & Ministry of Agricultural and Rural Affairs Key Laboratory of Molecular Biology of Crop Pathogens and Insect Pests, Institute of Insect Sciences, Zhejiang University, Hangzhou 310058, China

[2] Hainan Institute, Zhejiang University, Sanya 572000, China

[3] Senior Scientific Officer, Rice Farming Systems Division, Bangladesh Rice Research Institute, Gazipur, Bangladesh

Introduction

Over Earth's long history, the climate has changed radically, involving changes in temperature, precipitation, and carbon dioxide (CO_2) levels (Keller 2009). The Intergovernmental Panel on Climate Change (IPCC) consensus is that global temperatures have risen by 0.85 °C since 1880 and predicts an increase of ~ 0.3 °C– 4.8 °C by 2100, depending on the gas emission scenarios (IPCC 2014).

In addition, recent increases in heatwave frequencies and magnitudes indicate that with the increase in global average temperatures, extreme high-temperature events will be more frequent in the future (Hansen et al. 2012). Therefore, global warming poses diverse challenges to ecological processes that can reduce biodiversity, including insects (Nooten et al. 2014). Studies have shown that different species respond differently to changing temperatures, disrupting interspecies interactions and causing unexpected consequences for biodiversity and ecosystem functioning (Laws 2017; Pecl et al. 2017; Thierry et al. 2019; Tylianakis et al. 2008). Therefore, local or regional warming is one of the biggest challenges to agricultural ecosystem stability.

For poikilothermic organisms, especially insects, increasing environmental temperatures can pose serious challenges as their ability to regulate body temperature is limited. Elevated temperatures can directly affect the behavior, survival, development, reproduction, and other biological characteristics of insects (Angilletta 2009; Harrison et al. 2012) and further affect their population dynamics and distribution range (Gomez-Ruiz and Lacher 2019; Thuiller 2004). These changes are often accompanied by physiological and biochemical damage such as reduced water content, accelerated metabolism, and disordered nervous and endocrine systems (González-Tokman et al. 2020; Neven 2000). However, insects have also evolved various strategies to protect themselves from thermal stresses. One of the biochemical strategies is to synthesize a group of proteins called heat shock proteins (HSPs) (Arya et al. 2007). In insects, HSPs are mainly classified into four major families based on molecular weight and sequence homology: HSP90, HSP70, HSP60, and small HSP (sHSP) (King and MacRae 2015). As molecular chaperones, HSPs prevent irreversible denaturation and misfolding of cellular proteins and thus provide essential protection for insects under heat or other stresses (Chen et al. 2018; Colinet et al. 2010; Wang et al. 2012).

Rice (*Oryza sativa*) is the most important staple food crop globally and a major food source for over half the global population (Matsumoto et al. 2005). Since the 1960s, a class of small sap-sucking insects called planthoppers, especially the brown planthopper (BPH; *Nilaparvata lugens*), have emerged as the most destructive pests in rice fields due to the improper use of artificial fertilizers and insecticides since the Green Revolution (Bottrell and Schoenly 2012; Wu et al. 2020). Planthoppers can cause severe economic damages during rice production, directly by feeding and indirectly by transmitting several plant viral diseases (Sogawa 1982; Wang et al. 2017; Xue et al. 2014; Zhu et al. 2017a). The strong reproductive capacity and short development time of such *r*-strategist insect pests enable planthoppers to cause outbreaks and rapidly develop insecticide resistance under chemical control (Sogawa 2015). Thus, preserving natural biological control is considered key to prevent planthopper outbreaks.

The mirid bug, *Cyrtorhinus lividipennis*, a key biological control agent in paddy fields, feeds mainly on planthopper and leafhopper eggs and even some Lepidopteran pests (Heong et al. 1990; Jhansi Lakshmi et al. 2002; Zhu et al. 2014). *C. lividipennis* shows substantial predatory capacity for *N. lugens* eggs and is one of the most important predators in the rice ecosystem (Chua and Mikil 1989; Matsumura et al. 2005; Sivapragasam and Asma 1985). *Tytthus chinensis*, another mirid predator, also distributed in many rice-growing areas of China and Southeast Asia, exhibits similar hunting behavior and food preference as *C. lividipennis* (Henry 2012). Thus, these two niche-overlap mirid species might be competitive predators in rice fields, and both show strong intraguild predation (preying on another mirid) than extraguild predation (preying on *N. lugens*) in laboratory experiments (Qiao et al. 2016).

Many studies have shown that species in higher trophic levels seem more sensitive to increasing temperatures than species in lower trophic levels (Furlong and Zalucki 2017; Montserrat et al. 2013; Voigt et al. 2003). The unequal thermal effects on predators or parasitoids and pests may result in more frequent outbreaks of herbivores due to the decreasing predation and distribution range dissociation between them (Boukal et al. 2019). Additionally, heat tolerance varies among species, even though they share the same habitat. Therefore, the thermal tolerance of different mirid species warrants examination to understand how they respond to high-temperature conditions, which is important for biological control under elevated temperature conditions.

In this study, we compared the heat tolerance of *C. lividipennis* and *T. chinensis*. We investigated the effects of extreme heat stress and constant mild temperature on their survival, development, reproduction, and predation ability. We also observed the interspecific competition between two niche-overlap natural predators at simulated fluctuating temperatures to predict the occurrence of species population displacement due to global warming. In addition, we further analyzed the transcriptomes and *HSP* gene families as possible mechanisms underlying the varied thermal tolerance of the two mirids.

Materials and methods

Plant, insect, and equipment

Two mirid species, *C. lividipennis* and *T. chinensis*, and their prey BPH, *N. lugens*, were collected from the western paddy farm of Zijingang Western Campus, Zhejiang University, China. *N. lugens* were reared on susceptible rice seedlings cv. Taichung Native 1 (TN1), and *C. lividipennis* and *T.*

chinensis were reared separately in cages with fresh rice seedlings and sufficient prey (*N. lugens*). All the insects were placed in a controlled walk-in environmental chamber set at 26 °C ± 1 °C, 70% ± 10% relative humidity, and a 14:10 h light: dark photoperiod.

Next, 50-day-old TN1 rice plants cultured in nutrient solution (Yoshida et al. 1976) were used in bioassays. For all experiments (except for the choice and interspecific competition experiments), each biological replicate was performed in a glass tube (4.5 cm diameter and 25 cm height) containing one rice plant. Before the experiment, the temperature-controlled chambers were set to a specific temperature.

Thermal tolerance and geographic distributions of *T. chinensis* and *C. lividipennis*

The 50% lethal time ($LTim_{50}$) and lethal temperature ($LTem_{50}$) of *C. lividipennis*, *T. chinensis*, and *N. lugens* were measured to compare their heat tolerance. In the $LTim_{50}$ experiment, newly emerged female adults of the three species were exposed to 44 °C in an incubator to observe their survival at extreme temperature over time. For each biological replicate, 13–16 females were introduced to one rice plant, and for each species, at least 5 replicates were performed. The *N. lugens*-oviposited rice plants were used for mirids, while intact rice plants were used for *N. lugens*. The survival of each mirid species was recorded every 30 min during the first 4 h and then every 2 h until the end. To determine $LTem_{50}$, 15 female adults of each species were exposed to 26 °C, 30 °C, 34 °C, 38 °C, 40 °C, 42 °C, 43 °C, 44 °C, 45 °C, 46 °C, 47 °C, and 48 °C in an incubator, and the survival of each species was recorded after 60 min. $LTim_{50}$ and $LTem_{50}$ of each species were obtained by fitting logistic regression with Origin v8.5 software.

Distribution data of the two mirids were collected from previous descriptions (Henry 2012; Heong et al. 1995; Krishnaiah et al. 2007; Zhu et al. 2017b) and occurrence records with coordinates in the Global Biodiversity Information Facility (https://www.gbif.org/), and the integrated coordinate information was mapped using ArcGIS v10.7.

Effects of temperature on mirid fitness

Nymphal developmental durations of the two mirid species were monitored at constant temperatures of 18 °C, 22 °C, 26 °C, 30 °C, 32 °C, 34 °C, 35 °C, 36 °C, 38 °C, and 40 °C in a temperature-controlled incubator. We introduced the newly hatched nymphs (hatched in 12 h) individually into each egg-bearing rice plant, and at least 24 individuals were observed for each temperature treatment. The rice plant in each glass tube was replaced every 3–5 days. The developmental time of each individual was recorded until adult emergence as well as the number of nymphs that completed development at each temperature.

The development rate of each species at different temperatures was calculated and then fitted to Briere's model (Briere et al. 1999) using the Data Processing System (DPS) software v9.50 (Tang and Zhang 2013):

$$R(T) = \begin{cases} 0, T \le T_0 \\ aT\left(T - T_0\right)\left(T_L - T\right)^{\frac{1}{m}}, T_0 \le T \le T_L \\ 0, T \ge T_L \end{cases} \quad (1)$$

$$T_{opt} = \frac{(2mT_L + (m+1)T_0 + \sqrt{4m^2T_L^2 + (m+1)^2T_0^2 - 4m^2T_0T_L}}{4m+2} \quad (2)$$

In Eq. (1), R represents the development rate ($R = 1/d$, where d is the mean development duration in days), T is the experimental temperature in degrees °C, and a and m are empirical constants. The optimum temperatures of the two mirids were calculated by Eq. (2), where T_L indicates the upper threshold temperature and T_0 the lower threshold temperature.

Based on the performance of nymph development at different temperatures, we further determined the effects of 26 °C, 30 °C, 34 °C, and 38 °C on other biological parameters. One pair of newly emerged male and female adults was introduced to a *N. lugens* egg-bearing rice plant to observe the fecundity and longevity at each temperature. One glass tube with a pair of mirids was considered a replicate, and a total of 20 replicates were tested for each treatment. Survival of female adults was observed every 12 h, and rice plants were changed every 3–5 days. Mirid eggs in the replaced rice seedlings were counted under a stereomicroscope.

For body weight measurement, a pair of newly emerged mirids was introduced to one egg-bearing rice plant at different temperatures for 72 h. The female adult was then weighed using a Mettler Toledo balance (Model XS105DU; Mettler Toledo, Switzerland; $d = 0.01$ mg). More than 25 individuals of each species were weighed for each treatment.

To measure hatchability, 15 pregnant female adults were introduced to one rice plant with sufficient *N. lugens* eggs at rearing temperature (26 °C). After 12 h, the females were removed, and the plant was transferred to an incubator with a settled temperature (26 °C, 30 °C, 34 °C, and 38 °C). The rice plant was checked every 12 h for newly hatched nymphs. After hatching, the nymphs were counted and removed from the plant. When no newly hatched nymphs were observed for over 48 h, the plant was taken out of the glass tube and dissected under a stereomicroscope to check unhatched eggs. Hatchability was calculated using the following formula:

$$\text{Hatchability} = \frac{\text{Number of hatched nymphs}}{\text{Number of hatched nymphs} + \text{Number of unhatched eggs}}$$

The experiment was replicated 8–12 times for each species at each temperature.

We verified the normality and homogeneity of variance before performing analysis of variance (ANOVA). Two-way ANOVA followed by Tukey's multiple-range test ($P < 0.05$) was used to compare the differences in fecundity, longevity, body weight, and hatchability between *T. chinensis* and *C. lividipennis* at different temperatures.

Effects of temperature on the functional responses of the mirids

We used functional response experiments to measure the mirids' predatory behavior to *N. lugens* eggs. Different densities of gravid female adults of *N. lugens* were placed on rice plants for oviposition to create different egg densities varying from 1 to 200. Two-day-old female adults of *T. chinensis* and *C. lividipennis* were starved for 24 h and then introduced individually to the prepared *N. lugens* egg-bearing plants for another 24 h. The numbers of consumed and intact *N. lugens* eggs harbored in rice tissues (Fig. 3e) were counted under a stereomicroscope. At least 60 individuals of each species were tested for each temperature (26 °C and 38 °C).

Data from the functional response experiments were analyzed. First, the type of functional response of each treatment was determined using Juliano's method (Juliano 2001; Qiao et al. 2016) with Eq. (3).

$$\frac{N_a}{N_0} = \frac{\exp\left(p_0 + p_1 N_0 + p_2 N_0^2\right)}{1 + \exp\left(p_0 + p_1 N_0 + p_2 N_0^2\right)} \tag{3}$$

where N_a represents the number of eggs consumed by the mirids, N_0 is the initial number of *N. lugens* eggs, and p_0, p_1, and p_2 are estimated parameters. Past work has demonstrated that a non-significant linear coefficient p_1 indicates a type I response. Negative p_1 indicates that the predation rate of eggs monotonically declines with an increase in the initial egg number (N_0), showing a type II functional response. However, positive p_1 and negative p_2 indicate a type III functional response, with the predation rate initially increasing and then decreasing as N_0 increases (Juliano 2001). Since p_1 from all treatments was negative (Table S6 in Supplementary File 1), we fit the data with Holling's type II functional response Eq. (4) (Holling 1961):

$$\frac{N_a}{N_0} = \frac{aTN_0}{1 + aT_hN_0} \tag{4}$$

where T is the total available searching time, a represents the attack rate, and T_h is the handling time. Comparative analyses between different functional response groups were assessed by Eq. (5) (Juliano 2001):

$$N_a = \frac{\left[a + D_a(j)\right]TN_0}{1 + \left[a + D_a(j)\right]\left[T_h + D_{T_h}(j)\right]N_0} \tag{5}$$

where j is an indicator variable that takes values 0 and 1 for two comparison groups, respectively. D_a and D_{Th} are parameters estimating the differences in a and T_h values between treatments, respectively. The attack rate and handling time for one group were a and T_h, respectively, while for the other group, the attack rate was $a + D_a$ and the handling time was $T_h + D_{Th}$. If D_a (or D_{Th}) was significantly different from 0 (Student's t-test), the attack rate (or handling time) was significantly different between the two groups. However, if the D_a (or D_{Th}) was not significantly different from 0, there was no difference in the attack rate (or handling time) between the groups. All the parameters in Eqs. (3–5) of functional response analyses were estimated by fitting nonlinear regression with the accelerated simplex method (Nelder and Mead 1965) using DPS v9.50.

Effects of temperature on prey searching by mirids

To investigate the effects of high temperature on the mirids' foraging behavior and prey-locating

ability, we placed 10–15 female mirids in the middle of a petri dish between rice plants with and without *N. lugens* eggs (Fig. 3f) at 26 °C and 38 °C. All the mirids were starved for 24 h at 26 °C prior to the experiment. We counted the number of individuals on each rice plant after 0.5, 1, 2, 3, and 6 h. Each treatment had 8–10 biological replicates. The differences between temperature treatments and species at each time point were analyzed with one-way ANOVA followed by Tukey's multiple-range test ($P < 0.05$) using DPS v9.50.

Population growth rate at fluctuating temperatures and interspecific competition

The population growth of *T. chinensis* and *C. lividipennis* was investigated at fluctuating temperatures: 22 °C in

the dark and 26 °C in light (L26 °C:D22 °C); 26 °C in the dark and 30 °C in light (L30 °C:D26 °C); and 30 °C in the dark and 34 °C in light (L34 °C:D30 °C). A pair of newly emerged *T. chinensis* and *C. lividipennis* adults were introduced combinedly into the same well-ventilated plastic enclosure (10 cm diameter, 35 cm height) to observe the effects of different temperature regimes on the mirid population in the next generation under interspecific competitions, while *T. chinensis* or *C. lividipennis* adults were exposed separately to different temperature regimes for the treatment without competition. The mirids were allowed to lay eggs for 5 days, and the number of offspring that successfully reached the adult stage was counted for each species. Each treatment was replicated 6–9 times. Gravid *N. lugens* adults were introduced one day before the introduction of the mirids and the number of gravid BPH was kept at 8 during the entire experiment to ensure sufficient food for the mirids. Two-way ANOVA followed by Tukey's multiple-range test ($P < 0.05$) was performed to compare the differences in the offspring numbers between the two species at different fluctuating temperatures.

Transcriptome sequencing and annotation

Eggs, third instar nymphs, and newly emerged females of each mirid species were collected after exposure to 26 °C and 38 °C for 24 h. Three biological replicates were applied for each treatment. Samples were immediately frozen in liquid nitrogen before storing them at − 80 °C prior to RNA isolation. Total RNA was isolated using Trizol reagent (Invitrogen, Carlsbad, CA, USA) following the manufacturer's protocol. Illumina sequencing and complementary DNA (cDNA) library construction were performed at Novogene (Beijing, China). Clean data were obtained by removing adapters, low-quality reads, and high-content unknown base sequences and then de novo assembled using Trinity v.2.4.0 (Grabherr et al. 2011). Protein-coding sequences (CDS) were first searched using BLAST v2.2.28 + against Nr and Swiss-Prot databases, and if there was no match, predictions were made using ESTScan v3.0.3. Clean reads from different samples were mapped to the assembly using RSEM v1.2.15 (Li and Dewey 2011) to measure gene expression levels, and differential expression analyses were performed using DESeq2 v1.6.3 (Love et al. 2014).

HSP gene family analysis

HSP sequences of other insect species downloaded from the National Center for Biotechnology Information (NCBI) were used as query sequences to BLAST v2.2.28 + against the database constructed by predicted protein sequences of *T. chinensis* and *C. lividipennis* with a cut-off E-value of 1e − 5. Then, protein domains of sequences from the previous step were searched against the Pfam database using HMMER v3.0 (Eddy 2009). Finally, sequences with Pfam motifs of HSP90 (PF00183), HSP70 (PF00012), HSP60 (PF00118), and sHSP (PF00011) were considered as putative HSP sequences and confirmed manually.

For phylogenetic analysis, all putative HSP protein sequences from *T. chinensis* and *C. lividipennis* were aligned using ClustalW with default parameters. A phylogenetic tree was generated by MEGA v7.0.26 using the neighbor-joining (NJ) method with 1000 bootstraps. Motifs of the HSP sequences were identified from the MEME v5.3.0 website (https://meme-suite.org/) and displayed using TBtools v1.072 (Chen et al. 2020). Thermal stress-induced significantly upregulated genes in all stages were selected to further explore the expression patterns using quantitative polymerase chain reaction (qPCR). Gene-specific primers were designed by using Primer3 v0.4.0 (https://bioinfo.ut.ee/primer3-0.4.0/) and are listed in Table S12 (Supplementary File 1). Female adults of *T. chinensis* and *C. lividipennis* were sampled at different temperatures (26 °C, 30 °C, 34 °C, 38 °C, 40 °C, 42 °C, 44 °C, and 46 °C for 1 h) and different treatment times (1, 3, 6, 12, 24, 48, and 72 h at 38 °C). After treatment, total RNA was extracted from samples using Trizol reagent according to the manufacturer's protocol. Next, 1 μg of total RNA from each sample was reverse-transcribed into cDNA using the ReverTra Ace qPCR RT Master Kit with gDNA Remover (Toyobo, Japan). The relative transcript accumulation of genes was measured using the Bio-Rad CFX96 Real-Time System (Bio-Rad Laboratories, Hercules, CA, USA) and the SYBR Green Real-Time PCR Master Mix (Toyobo). Three biological replicates (5 individuals per sample) for each treatment were performed, and *tubulin* genes of each species were used as the internal standard for normalization.

Reverse transcription qPCR (RT-qPCR) results, logarithmic transformation was performed to fit the normal distribution, and differences among different treatment times and temperatures were analyzed using one-way ANOVA followed by Fisher's least significant difference test ($P < 0.05$) with DPS v9.50. Figures were prepared using GraphPad Prism v7.0.0 and compiled using Adobe Illustrator CC 2018.

Results

Thermal tolerance of two mirids and their prey *N. lugens*

Logistic regressions of the survival rate showed different trends across *T. chinensis*, *C. lividipennis* and their prey *N. lugens* at 44 °C (Fig. 1a). *C. lividipennis* exhibited the weakest tolerance to extreme heat; all individuals died within

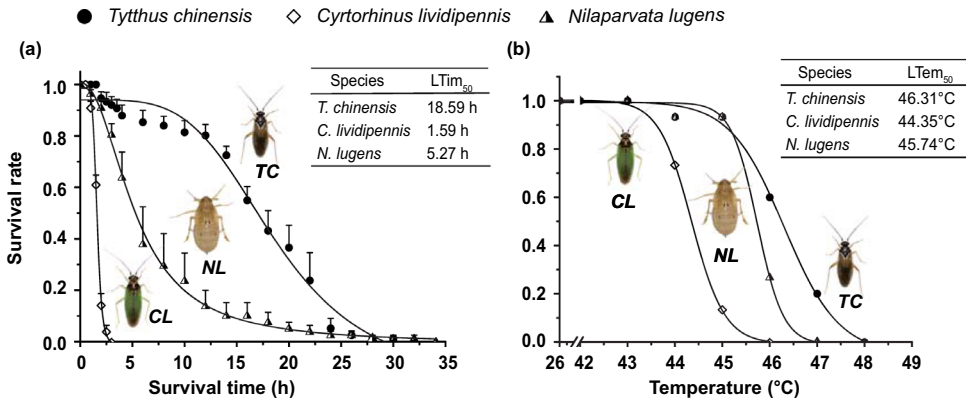

Fig. 1 $LTim_{50}$ and $LTem_{50}$ of *Tytthus chinensis, Cyrtorhinus lividipennis* and *Nilaparvata lugens*. The curves were fitted by logistic regression based on observation data of the species' survival rates at **a** different times under 44 °C and **b** different temperatures in 60 min. Different symbols represent mean values in different species, whereas the vertical line above the symbol stands for the standard error. Tables show $LTim_{50}$ or $LTem_{50}$ of the species. *TC*, *T. chinensis*; *CL, C. lividipennis*; *NL*, *Nilaparvata lugens*; $LTim_{50}$, 50% lethal time; $LTem_{50}$, 50% lethal temperature

3 h, and $LTim_{50}$ was only 1.59 h. For *N. lugens*, the fitting curve decreased more gently and $LTim_{50}$ was 5.27 h, indicating better heat resistance than *C. lividipennis*. *T. chinensis* showed the most substantial heat tolerance, with the highest $LTim_{50}$ of 18.59 h, which was more than 11 and 3 times longer than its competitor (*C. lividipennis*) and prey, respectively. In addition, *T. chinensis* exhibited the highest $LTem_{50}$ of 46.31 °C which was 1.96 °C and 0.57 °C higher than that of *C. lividipennis* (44.35 °C) and *N. lugens* (45.74 °C), respectively (Fig. 1b). The available data showed a large overlap in the geographic distribution of the two mirid predators in Asia–Pacific areas, which was also coincident with the distribution of *N. lugens* (Dyck and Thomas 1979) (Fig. S1 in Supplementary File 1). The coordinate information of the two mirid species is given in Supplementary File 2.

Effects of high temperature on the fitness of the two mirids

The development rates of the *T. chinensis* and *C. lividipennis* nymphs fitted well with Briere's model (Fig. 2a), and all the estimated parameters are presented in Table S3 (Supplementary File 1). Based on the fitting curve, the developmental rate of *C. lividipennis* increased gradually from 12.58 °C (T_0) to 32.83 °C (T_{opt}) and then suddenly decreased to 0 at 36.11 °C (T_L). A similar trend of the fitting curve was observed in *T. chinensis*, but its T_{opt} (34.57 °C) and T_L (40.28 °C) were significantly higher compared with *C. lividipennis*. Compared with *C. lividipennis*, *T. chinensis* nymphs completed their development in a much wider temperature range and grew faster at high temperatures. The survival rates of the two species were observed to peak at 26 °C (*C. lividipennis*) and 30 °C (*T. chinensis*) (Table S4 in Supplementary File 1), which were lower than their optimum developmental temperatures.

The impact of temperature on the mirid body weight significantly differed among the temperature treatments ($F_{3,198}=39.446$, $P<0.01$), mirid species ($F_{1,198}=7.659$, $P<0.01$), and their interactions ($F_{3,198}=13.464$, $P<0.01$) (Fig. 2b). Both species reached the highest body weights at 30 °C (*T. chinensis*: 1.38 mg, *C. lividipennis*: 1.55 mg) and the lowest at 38 °C (*T. chinensis*: 1.25 mg, *C. lividipennis*: 1.11 mg). At 26 °C, 30 °C, and 34 °C, the *C. lividipennis* body weight was significantly higher than that of *T. chinensis*. Nevertheless, *T. chinensis* gained a significantly higher body mass compared with *C. lividipennis* at 38 °C (Table S5 in Supplementary File 1).

The longevity of the mirids was also affected differently by temperature treatments ($F_{3,152}=34.204$, $P<0.01$), but no significant differences were observed between species ($F_{1,152}=0.766$, $P=0.383$) and temperature × species interactions ($F_{3,152}=1.226$, $P=0.302$) (Fig. 2c). The longevity of *T. chinensis* was similar at 26 °C and 30 °C; however, the survival time significantly decreased with a further increase in temperature. The longevity of *C. lividipennis* adults was also significantly lower at 38 °C compared to other temperature treatments. There was no significant difference in the female life span between the two species at any temperature (Table S5 in Supplementary File 1).

Similar to longevity, mirid fecundity was significantly affected by temperature treatments ($F_{3,152}=37.773$, $P<0.01$), but no significant differences were observed between species ($F_{1,152}=1.306$, $P=0.255$) and the temperature × species interaction ($F_{3,152}=2.472$, $P=0.064$). As shown in Fig. 2d, temperature increase had a serious effect on the total eggs laid in both species, which decreased

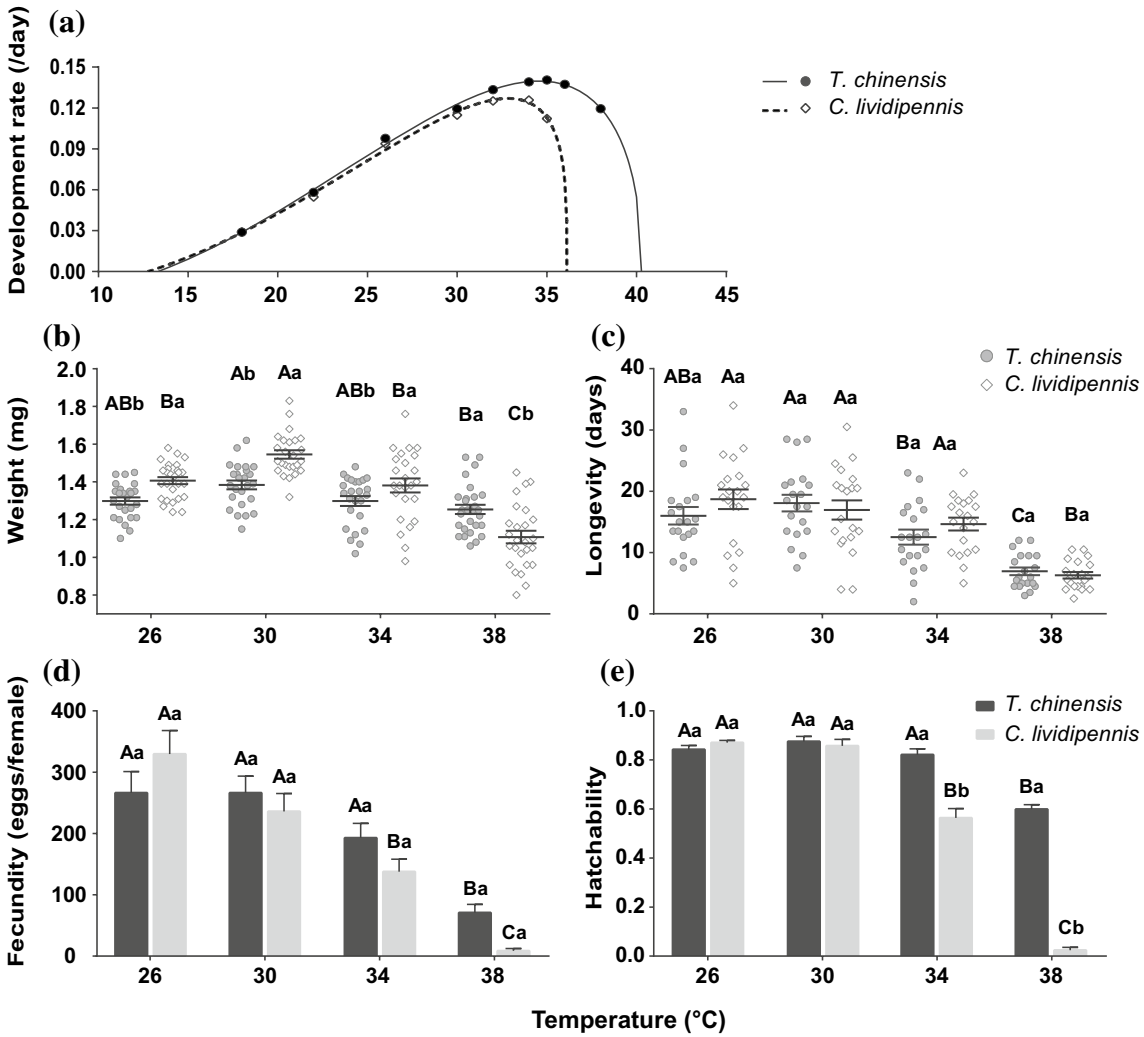

Fig. 2 Effect of different temperatures on the fitness of *Tytthus chinensis* and *Cyrtorhinus lividipennis*. **a** The fitting curves illustrate the nymph development rate of two species under a series of temperatures using Briere's model. **b** Body weight, **c** longevity, **d**, fecundity and **e** hatchability of the two species at 26 °C, 30 °C, 34 °C, and 38 °C. Bars indicate means ± standard error, and dots in **b** and **c** represent individual observations. Capital letters indicate the comparison among different temperatures within a given mirid species, and lowercase letters indicate the comparison between the two species at a given temperature. Different letters represent significant differences at $P < 0.05$

by 73.37% (*T. chinensis*) and 97.36% (*C. lividipennis*) from 26 °C to 38 °C (Table S5 in Supplementary File 1).

The effect of temperature on hatchability was significantly different among temperature treatments ($F_{3,71} = 257.504$, $P < 0.01$), mirid species ($F_{1,71} = 159.308$, $P < 0.01$), and temperature × species interactions ($F_{3,71} = 92.334$, $P < 0.01$) (Fig. 2e). The hatchability of *T. chinensis* was significantly lower at 38 °C compared to other temperature treatments. In *C. lividipennis*, egg hatching was similar at 26 °C and 30 °C; however, hatchability significantly decreased with a further increase in temperature. Comparing to 26 °C, the hatchability of *T. chinensis* and *C. lividipennis* reduced by 28.86% and 97.24%, respectively, when exposed to 38 °C, indicating varied heat damage in the two species (Table S5 in Supplementary File 1).

Effects of high temperature on predatory capacity

The food consumption of predators represents their predation potentials as biological control agents. Heat stress might have different effects on the predation ability of different predators, leading to different pest control efficiency. Functional response is a widely used and intuitive method of assessing and comparing the predation ability or parasitism efficiency between different natural enemy species or different treatments (Bodino et al. 2018; Farrokhi et al.

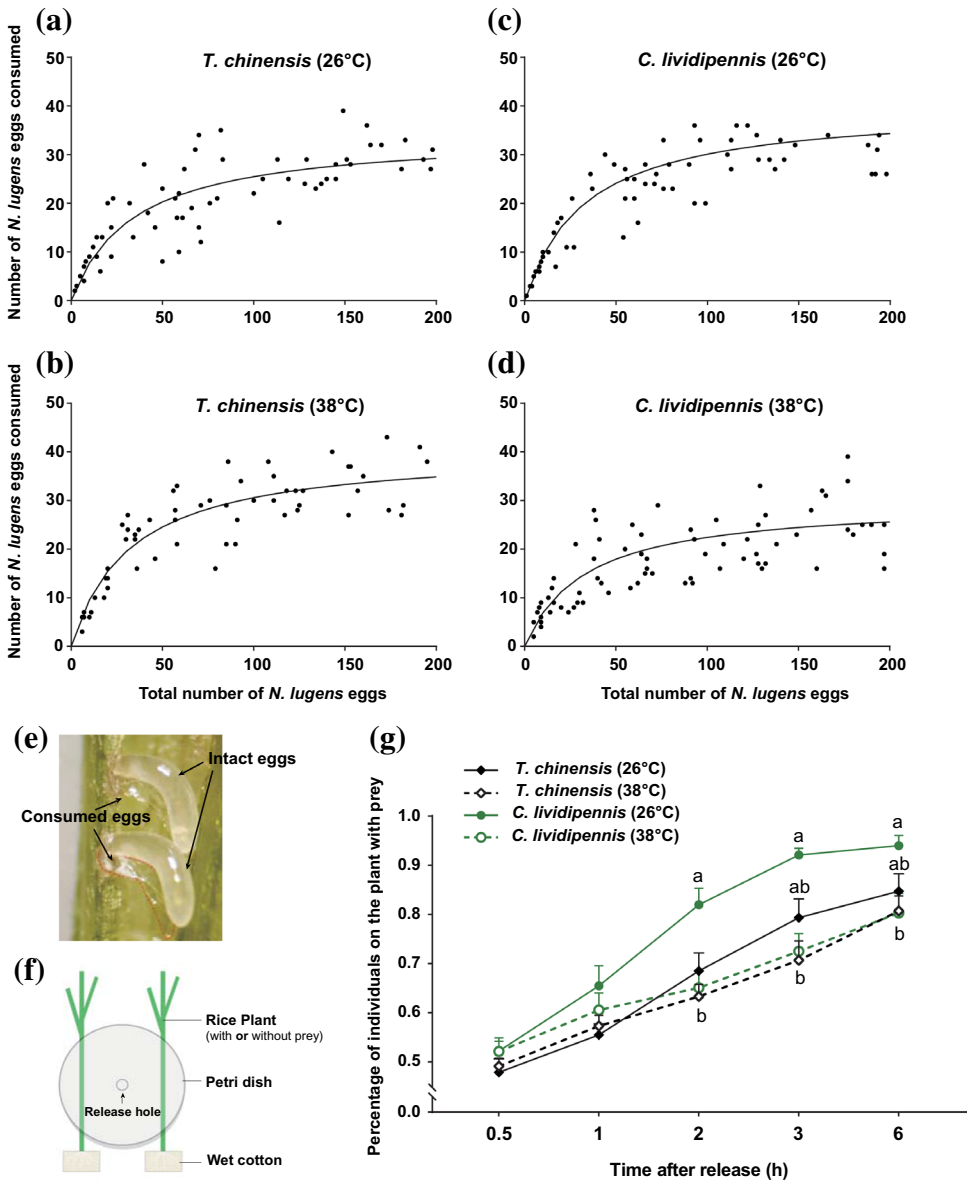

Fig. 3 Functional responses and prey location of *Tytthus chinensis* and *Cyrtorhinus lividipennis* under normal- and high-temperature conditions. Functional response of *T. chinensis* female adults at **a** 26 °C ($n=63$) and **b** 38 °C ($n=60$). Functional response of *C. lividipennis* female adults at 26 °C **c** ($n=62$) and **d** 38 °C ($n=73$). **e** Consumed and intact *Nilaparvata lugens* eggs after functional response experiments. **f** Equipment used for the prey-locating experiment. **g** Proportion of individuals of the two mirid species settling on the rice plant with prey at different temperatures over time. Different letters represent significant differences at $P<0.05$ at each time point

Table 1 Estimated parameters for functional responses of *T. chinensis* and *C. lividipennis* at different temperatures

Species	Temperature (°C)	r^2	P	Attack rate ± SE (/day)	Handling time ± SE (day)	Maximum predation
T. chinensis	26	0.7032	< 0.001	0.9920 ± 0.1699	0.0292 ± 0.0021	34.25
C. lividipennis	26	0.8304	< 0.001	1.2155 ± 0.1624	0.0273 ± 0.0014	36.63
T. chinensis	38	0.7835	< 0.001	1.2486 ± 0.1611	0.0247 ± 0.0013	40.49
C. lividipennis	38	0.5787	< 0.001	0.8972 ± 0.1704	0.0335 ± 0.0026	29.85

r^2 is the coefficient of determination

P value was determined by F-test of overall significance in regression analysis

2010; Zamani et al. 2006). Therefore, we compared the functional responses of *T. chinensis* and *C. lividipennis* at 26 °C and 38 °C.

All treatments showed a type II functional response, with significantly negative p_1 values (Table S6 in Supplementary File 1). The fitted curves and estimated parameters are presented in Fig. 3 a–d and Table 1, respectively.

Table 2 Comparative analysis of functional responses between species and temperatures

Factor	Comparison	$D_a \pm SE$ (*P*)	$D_{Th} \pm SE$ (*P*)
Temperature	26 °C vs 38 °C (*CL*)	0.3183 ± 0.1624 (0.0545, NS)	−0.0062 ± 0.0014 (< 0.001, **)
	26 °C vs 38 °C (*TC*)	−0.2566 ± 0.1699 (0.1361, NS)	0.0045 ± 0.0021 (0.0352, *)
Species	*TC* vs *CL* (26 °C)	−0.2235 ± 0.1699 (0.1933, NS)	0.0019 ± 0.0021 (0.3698, NS)
	TC vs *CL* (38 °C)	0.3514 ± 0.1611 (0.0332, *)	−0.0088 ± 0.0013 (< 0.001, **)

NS no significance, $*P < 0.05$, $**P < 0.01$

TC T. chinensis, *CL C. lividipennis*

The numbers of eggs consumed by the mirids increased with prey density, but the proportion of eggs consumed declined with increasing prey density in all treatments. The maximum predation with each treatment was calculated by T/T_h, representing the maximum number of eggs that each mirid could prey on daily. *C. lividipennis* showed higher predation at 26 °C, with a maximal daily predation of 36.63 eggs, whereas *T. chinensis* exhibited higher egg consumption at 38 °C (40.49 eggs).

The attack rates and handling times of both species were compared at different temperatures (Table 2). The predatory ability of *C. lividipennis* was negatively impacted by high temperatures, with a significantly longer handling time at 38 °C. In contrast, the handling time of *T. chinensis* decreased at 38 °C, indicating they spent less time on each prey. Comparative analysis between species showed no significant difference in attack rates or handling times at 26 °C, although *T. chinensis* showed a better hunting capacity with a significantly higher attack rate and lower handling time compared with *C. lividipennis* under thermal stress.

The prey-locating ability of *T. chinensis* was not affected by the high temperatures at any time point (Fig. 3g); however, heat stress had more obvious effects on the prey locating ability of *C. lividipennis*. The positive choice rates (proportion of mirids settled on rice plants with *N. lugens* eggs) of *C. lividipennis* at high temperature started decreasing after 2 h and continued up to 6 h. At all time points, there was no significant difference in positive choice rates between the two species at 38 °C. However, *C. lividipennis* exhibited a better prey locating efficiency than *T. chinensis* at 26 °C, and a significant difference was observed at 2 h after release.

Effects of fluctuating temperature and interspecific competition on population growth

To better understand the effects of temperature on *T. chinensis* and *C. lividipennis* and their interactions in the field, we observed the population changes in each species in different fluctuating temperature regimes and competitive conditions. The number of offspring significantly differed among the different temperature regimes ($F_{2,41} = 5.494$, $P < 0.01$) and temperature × species interaction ($F_{2,41} = 4.944$, $P = 0.012$) but not between species

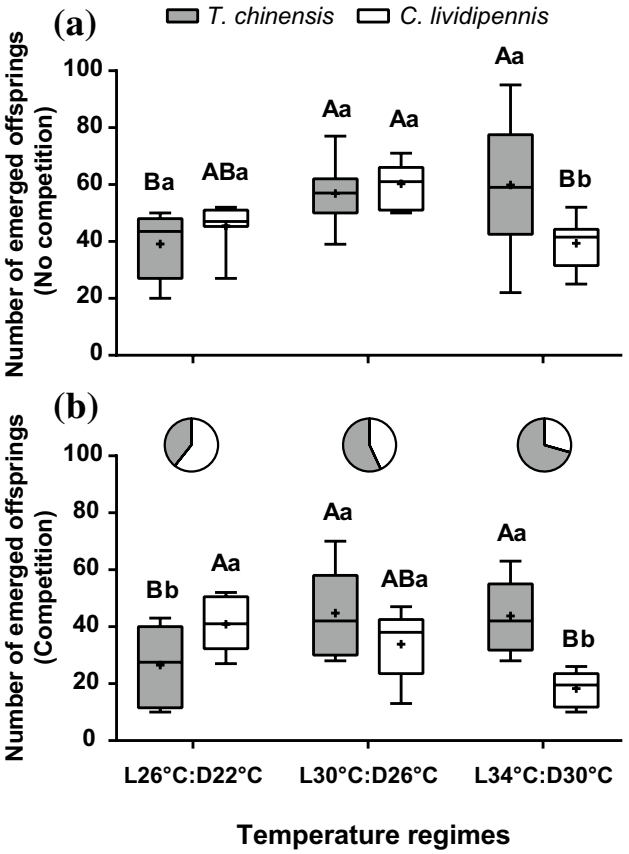

Fig. 4 Effects of fluctuating temperatures and interspecific competition on population growth of *Tytthus chinensis* and *Cyrtorhinus lividipennis*. The numbers of emerged offspring of two mirids at different temperature regimes **a** without or **b** with interspecific competition. L26°C:D22°C means 26 °C in light for 14 h and 22 °C in the dark for 10 h. L30°C:D26°C denotes 30 °C in light for 14 h and 26 °C in the dark for 10 h, and L26°C:D22°C represents 34 °C in light for 14 h and 30 °C in the dark for 10 h. Boxplots display mean values (+), median lines, interquartile ranges, and whiskers (min. to max.). Pie charts in **b** show the proportions of the two species under different treatments when they co-persisted. Capital letters indicate the comparison among different temperature regimes within a given mirid species, and lowercase letters indicate the comparison between the two species within at a given temperature. Different letters represent significant differences at $P < 0.05$

($F_{1,41} = 1.160$, $P = 0.288$) (Fig. 4a). The number of *T. chinensis* offspring was significantly lower at L26 °C:D22 °C compared to other temperature treatments, while the

C. lividipennis population was significantly higher at L30 °C:D26 °C compared to L34 °C:D30 °C. Under high-temperature conditions (L34 °C:D30 °C), the *T. chinensis* population was higher than that of *C. lividipennis*, whereas there was no significant difference in the offspring number of two species in other temperature regimes.

When the two species co-persisted, the effects on populations significantly differed between them ($F_{1,40} = 6.86$, $P = 0.012$) and also in the temperature × species interactions ($F_{2,40} = 9.249$, $P < 0.01$) (Fig. 4b). Different fluctuating temperature regimes influenced interspecific competition between the two species. Under lower temperature conditions (L26 °C:D22 °C and L30 °C:D26 °C), *C. lividipennis* was more competitive and constituted the major proportion of the total population. However, *T. chinensis* was more aggressive under the high-temperature conditions (L34 °C:D30 °C) and secured a higher proportion of the total population (pie charts in Fig. 4b).

Identification of *HSPs* in two predators

We sequenced the transcriptomes of eggs, nymphs, and adults of *T. chinensis* and *C. lividipennis* at 26 °C and 38 °C to explore the molecular mechanisms underlying their different responses to heat stress. Based on the differentially expressed gene analyses, several *HSP* genes were upregulated after thermal stress in both species (Tables S9 and S10 in Supplementary File 1), suggesting that this gene family might play an important role in heat resistance. A total of 19 and 17 *HSP* genes were identified in *T. chinensis* and *C. lividipennis* (Fig. 5a and Table S11 in Supplementary File 1), respectively. The *HSP* gene family

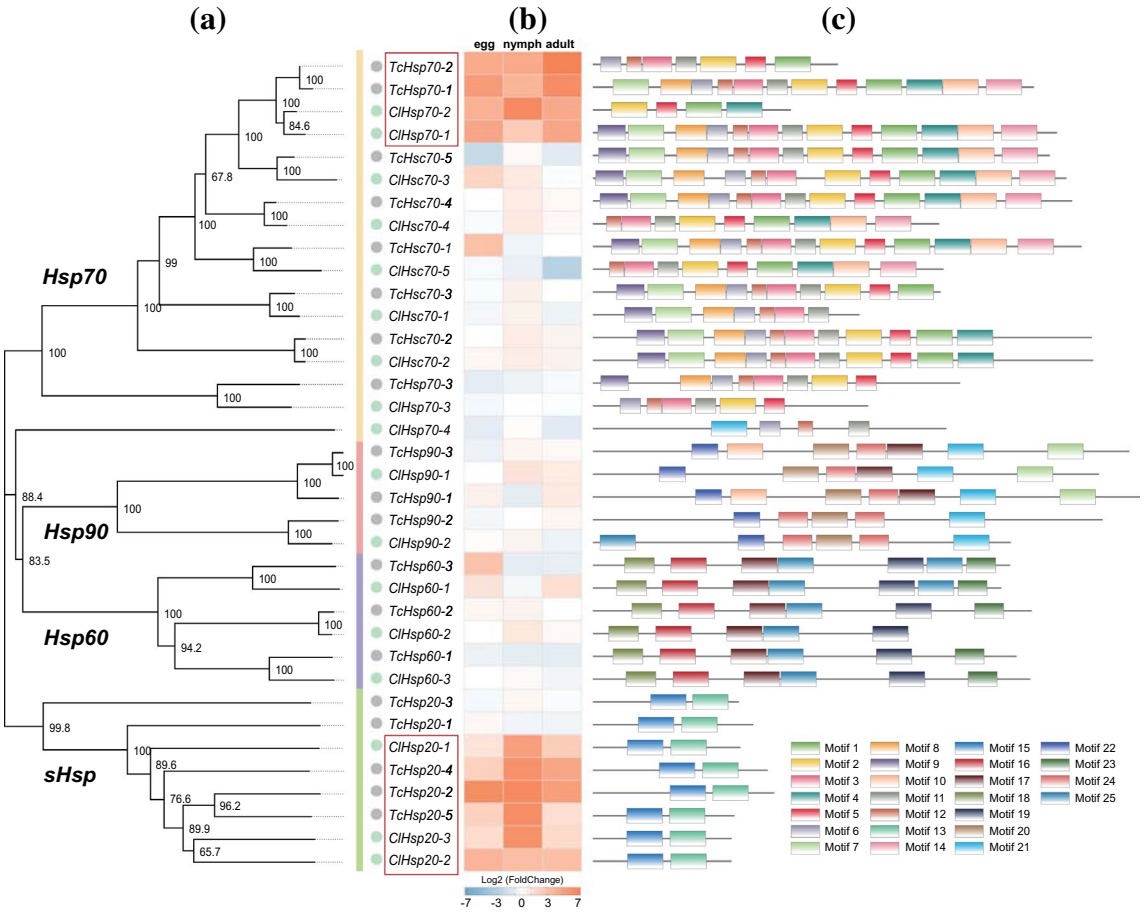

Fig. 5 Phylogenetic relationships, expression profiles, and protein motif analyses of *HSP*s from *Tytthus chinensis* and *Cyrtorhinus lividipennis* based on transcriptome analysis. **a** The phylogenetic tree was constructed using MEGA 7 by Neighbor-Joining method with 1000 bootstraps. Numbers on branches are bootstrap percentages based on 1000 replicates. Different color strips next to the phylogenetic tree indicate different *Hsp* gene families. The gray or green circle in front of the gene name represents that the gene was identified from *T. chinensis* or *C. lividipennis*, respectively. **b** The heat map shows the expression fold changes of *HSPs* at different life stages of two mirids after heat exposure (38 °C as heat treatment, 26 °C as control). The fold changes ($\log_2$) of *HSPs* are shown in different colors: red, white, and blue indicate upregulated, no change, and downregulated gene expression, respectively. Genes showing significant upregulation at all stages are enclosed in red boxes. **c** All motifs of HSPs were identified using MEME v5.3.0. HSP, heat shock protein

included 3 *HSP90s*, 8 *HSP70s*, 3 *HSP60s*, and 5 *sHSPs* in *T. chinensis* and 2 *HSP90s*, 9 *HSP70s*, 3 *HSP60s*, and 3 *sHSPs* in *C. lividipennis*. CDS and protein sequences of *HSP* genes are given in Supplementary Files 3 and 4. Phylogenetic tree analysis revealed that HSP sequences from each family were highly conserved among species and clustered in four branches (except *ClHsp70-4*) (Fig. 5a). In addition, proteins that belong to the same families showed similar motif constitutions (Fig. 5c), and the details of these motifs are listed in Table S13 (Supplementary File 1). In both mirids, 2 *HSP70s* and 3 *sHSPs* (Fig. 5b, red boxes) were highly upregulated at all stages, indicating that these genes might have potential functions in heat responses and were, therefore, selected for further analysis.

Expression patterns of *HSPs* in response to thermal stress

RT-qPCR analysis revealed that all *HSP* genes in *T. chinensis* were significantly upregulated at 38 °C, and their expression levels increased with a further increase in temperature but decreased at 46 °C, which was close to $LTem_{50}$ (46.31 °C). For *C. lividipennis, HSP* genes also showed similar expression patterns as in *T. chinensis*; however, the expression started to decline at a lower temperature (44 °C) compared to *T. chinensis*, although this temperature was also close to $LTem_{50}$ of *C. lividipennis* (44.35 °C). In addition, the inductions of *HSP* genes were much stronger in *T. chinensis* (*TcHsp70-1, TcHsp70-2, TcHsp20-2, TcHsp20-4* and *TcHsp20-5* expressed 1311-, 5219-, 423-, 1185- and 30-fold increases, respectively, when they peaked at 44 °C) than in *C. lividipennis* (*ClHsp70-1*, *ClHsp70-2*, *ClHsp20-1*, *ClHsp20-2*, and *ClHsp20-3* expressed 292-, 2176-, 237-, 71 and 13-fold increases, respectively, when they peaked at 42 °C) under heat treatments (Figs. 6a and b).

Further, the expression of *HSP* genes at different time points revealed that most of the genes (*TcHsp70-1, TcHsp70-2, TcHsp20-2,* and *TcHsp20-4*) were significantly upregulated in *T. chinensis* within 1 h and then were gradually downregulated over time (Fig. 6c). In comparison, the expression patterns of *C. lividipennis HSP* genes at different time points varied among genes. *ClHsp70-1* induction was relatively stable up to 24 h and then slightly decreased after 48 h. *ClHsp70-2*, *ClHsp20-2*, and *ClHsp20-3* expression peaked at 12, 24, and 12 h, respectively, and then gradually

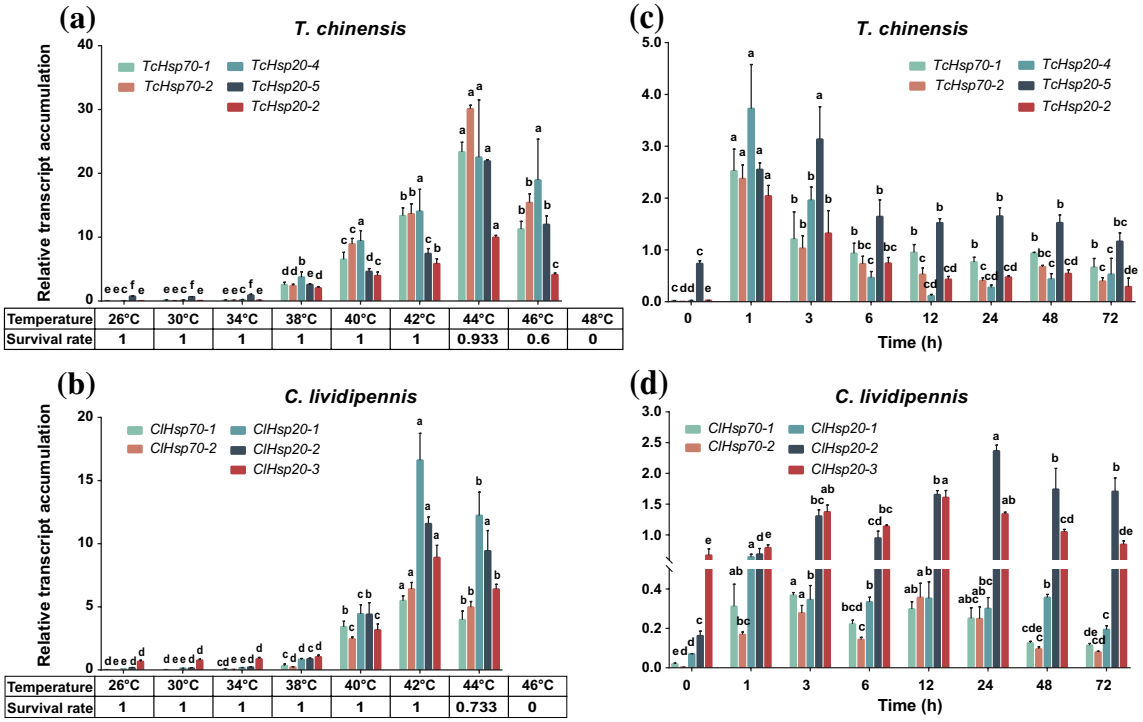

Fig. 6 Expression patterns of *HSP* genes in *Tytthus chinensis* and *Cyrtorhinus lividipennis* after treatment with different temperatures and exposure times. **a**, **b** *HSP* gene expression patterns and survival rates of two mirids at different temperatures for 1 h. The observed survival rates at different temperatures are listed below the horizontal axis (Table S2 in Supplementary File 1). **c**, **d** *HSP* gene expression patterns of the two mirids treated with 38 °C for different exposure periods. 0 h represents no heat treatment. Bars indicate means ± standard error. Different letters indicate significant differences in the expression of the gene among different temperatures or time points ($P < 0.05$). HSP, heat shock protein

declined with an increase in treatment time. Only *ClHsp20-1* reached the highest transcript accumulation within the first hour of treatment (Fig. 6d).

Discussion

Organisms can be affected by both average temperature increases as well as extreme temperatures (Hay et al. 2016). With climate change, average temperatures and extreme weather events will rise with increasing frequency in large parts of Asia, including many rice-growing regions (IPCC 2014). We assessed $LTim_{50}$ and $LTim_{50}$ of three species (*T. chinensis*, *C. lividipennis*, and *N. lugens*), which could indicate their ability to respond to increasing extreme-temperature events, an intuitive index comparing the thermal resistance among species. Of the three tested species, *C. lividipennis* exhibited the highest sensitivity to heat stress and even a short period of extreme high temperature was fatal. Both extreme-temperature events and increasing average temperatures would possibly cause more damage to *C. lividipennis* than to its prey *N. lugens*. Many organisms have to shift their distribution in adapting to global warming (Perry et al. 2005; Rushing et al. 2020; Sanchez-Guillen et al. 2016), and climate-related local extinctions have already occurred in hundreds of species (Wiens 2016). Therefore, different heat resistance might result in a geographic mismatch between predator and prey, eventually leading to the pests being released from the control of their natural enemies in some areas. In contrast, *T. chinensis* showed greater heat tolerance than both its competitor (*C. lividipennis*) and prey (*N. lugens*), so it might become a valuable ecosystem service provider under more extreme-temperature conditions. Unfortunately, the available distribution data of the two mirids are still limited, especially for *T. chinensis*. Compared to the dominant predator *C. lividipennis*, researchers have paid much less attention to *T. chinensis* (probably the reason this species is not recorded in many landmasses of China); therefore, the information about the two species might be asymmetrical. With more comprehensive and accurate distribution information, we would be able to further analyze the correlation between the distribution and thermal tolerance of *T. chinensis* and *C. lividipennis* and predict the range shifts of the two predators and their prey under global warming to better understand the impact of climate change on biological control.

The nymphs of the two mirids seem more vulnerable to temperature changes. Even young nymphs can help control planthoppers by preying on their eggs (Qiao et al. 2016). However, the lack of protection from host plants (compared to the eggs that harbored in the plant tissue), fragile exoskeletons, and weak mobility (compared to adults) make it more challenging for the nymphs to resist various biotic and abiotic stresses compared with individuals at other stages. *C. lividipennis* and *T. chinensis* were unable to complete their full development at 36 °C and 40 °C, respectively (Table S4 in Supplementary File 1). We fitted Briere's equation and found that the estimated upper thresholds (T_L) of the two species (36.11 °C for *C. lividipennis* and 40.28 °C for *T. chinensis*) were highly consistent with experiment data, therefore reflecting the great reliability of this model. The *m* parameter was interpreted as the capacity of an insect species to develop and survive close to its lethal temperature (Briere et al. 1999). The lower *m* value coupled with higher the T_{opt} and T_L of *T. chinensis* implies higher heat tolerance of *T. chinensis* nymphs compared with its competitor and therefore more capable to survive the hot summer months.

Compared with *T. chinensis*, *C. lividipennis* possessed a relatively larger body size, higher longevity, and stronger reproductive ability at 26 °C which could contribute to its current dominance in most of the paddy fields. Although constant high temperatures negatively influenced the development and reproduction of both mirid species, *C. lividipennis* suffered more with a much lower body weight and a loss in egg hatchability and fecundity under high-temperature conditions. Reproductive ability plays an important role in population maintenance, so the different effects of heat stress on the reproduction of *T. chinensis* and *C. lividipennis* might differently affect their field populations as the temperature increases.

As important natural enemies, the predation ability of mirids under high-temperature conditions might be of concern. Our data revealed that higher attack rates and shorter handling times of *C. lividipennis* at 26 °C (but not significant) are consistent with the findings of Qiao (Qiao et al. 2016). Normally, metabolism of arthropods increases with temperature, and more energy is needed for normal life activities (Brown et al. 2004; González-Tokman et al. 2020). Therefore, many predators show stronger predation abilities under higher but tolerable temperature conditions (de Mira-Mendes et al. 2019; Frank and Brambock 2016; Schwarz and Frank 2019), which was also observed in *T. chinensis* at 38 °C. While *C. lividipennis* consumed significantly fewer prey, which obviously could not meet its increasing energy demands and eventually led to a significantly reduced body weight (Fig. 2b) at 38 °C. Elevated temperatures seriously threaten predation by *C. lividipennis*, indicating that the pest suppression efficiency of *C. lividipennis* might be severely affected during the hot summer months, especially during a heatwave. However, how temperature differentially affects olfactory perception, metabolic rate, digestive enzyme activity, and other physiological processes in the two species deserve further comparative research.

Fluctuating temperatures in the field cause physiological, life history, and ecological effects on insects different from predictions in the laboratory (Colinet et al. 2015).

A relatively mild and fluctuating temperature regime (L34°C:D30°C, daily average temperature: 32.33 °C) still caused a significant population decline in *C. lividipennis*, which was not observed in *T. chinensis*. Due to the similar foraging ecology, the co-occurrence of two mirids in the fields was common. Under the heat stress (L34 °C:D30 °C) conditions, differences in the population growth rate were more obvious with interspecific competition than in treatment without interspecific competition. This indicated that the asymmetric effects of increasing temperature on the two mirids might not only affect their fitness and predatory capacity but also interspecific interactions. These two similar predators are not only competitors for the same herbivore prey but also exhibit strong intraguild predation (IGP) on each other, which is common between many competitive natural enemies (Khan and Yoldas 2018; Perdikis et al. 2014; Yu et al. 2019). An increase in IGP intensity with increasing temperature has been observed in some aquatic predators (Frances and McCauley 2018). The IGP performances of the two mirids might also be affected by temperature, further intensifying the interspecific competition. This could contribute to the dominance of the more competitive species when the two mirids co-persist under different temperature conditions (*C. lividipennis* dominance in L26 °C:D22 °C, *T. chinensis* dominance in L34 °C:D30 °C). Therefore, interspecific interactions under different temperature conditions might eventually lead to different outcomes such as population variation or even population displacement. However, longer-term studies, such as simulated field warming experiments, may provide more valuable information about the possibility of population displacement due to global warming.

The importance of *HSP* gene families in the thermal adaption of organisms is well documented (Feder and Hofmann 1999; King and MacRae 2015; Wang et al. 2004). We also found that many *HSP* genes were upregulated in both *T. chinensis* and *C. lividipennis* under heat stress (Tables S9 and S10 in Supplementary File 1). *HSP70s* and *sHSPs* seem to play more important roles than *HSP90s* and *HSP60s* in the heat tolerance of many insect species, such as *Bemisia tabaci* (Wang et al. 2019), *Bombyx mori* (Guo et al. 2018), and *Cnaphalocrocis medinalis* (Quan et al. 2020). Similarly, in *T. chinensis* and *C. lividipennis*, respectively, 5 genes from *HSP70* and *sHSP* gene families were induced after heat treatments at all life stages. In addition, the induced genes were found clustered together in each gene family clade, suggesting that similar sequence structures might determine similar functions in resisting thermal stress.

The expression of *HSP* genes in both species increased and then decreased with increasing temperature (Figs. 6a and b). A similar expression pattern was also found in the maize weevil *Sitophilus zeamais*. The relative transcript accumulation of *HSP* genes in the weevil increased significantly with increasing temperature but reduced at the lethal temperature of 45 °C when the survival rates at all stages declined (Tungjitwitayakul et al. 2015). In addition, a previous study on two *Liriomyza* species suggested that the onset and maximal induction temperature of *HSP* gene expression might represent the differences in thermal tolerance of species (Huang and Kang 2007). Although we did not observe a difference in onset temperature between *T. chinensis* and *C. lividipennis* (probably due to the large interval between the first few temperatures), the higher maximal induction temperature of *HSP* gene expression in *T. chinensis* was apparently consistent with its better thermal tolerance. The *HSP* genes in *T. chinensis* also exhibited higher expression levels and shorter induction times compared with *C. lividipennis* which could contribute to more rapid and substantial production and accumulation of heat shock proteins in *T. chinensis* to reduce damage from high temperatures to cells and protein molecules, helping it better resist heat stress.

Conclusion

The dominant predator *C. lividipennis* displays much weaker heat resistance than its prey *N. lugens*, which might lead to unsynchronized population variations in the two species with temperature increase. However, *T. chinensis*, another predator in the rice ecosystems with similar habits, exhibits better tolerance and adaptability compared with *C. lividipennis* which might be related to a variation in *HSP* gene induction. The stronger predatory ability of *T. chinensis* highlights its importance as a biological control agent under high-temperature conditions in the future. Moreover, the stronger competitive ability of *T. chinensis* under heat stress indicates that high temperatures might also affect the interactions between *T. chinensis* and *C. lividipennis* and possibly lead to population displacement in hot areas and seasons due to global warming.

Author contributions

YLB and ZRZ conceived and designed experiments. YLB performed the experiments. YLB and MKQ analyzed data. YLB wrote the manuscript. MKQ, WWZ and ZRZ contributed to the critical revision of the manuscript. All the authors revised and approved the manuscript.

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Availability of data and material Transcriptome data were deposited in the Sequence Read Archive (SRA) repository of NCBI (accession numbers: PRJNA699971, PRJNA699972). All bioassay data, distribution information and identified heat shock protein sequences can be found in Supplementary Information files.

Declarations

Conflicts of interest The authors have declared that they have no conflict of interest.

Ethics approval This article does not contain any studies with human participants or vertebrates performed by any of the authors.

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