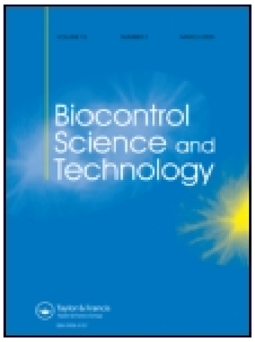

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RESEARCH ARTICLE

Effect of short-term high temperature stress on the development and fecundity of *Ophraella communa* (Coleoptera: Chrysomelidae)

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Since insects are ectothermic, they are highly vulnerable to the sudden increase of temperature. Indeed, it has been hypothesized that the survival, development, fecundity, and even population expansion of insects are all affected significantly by extremely high temperature. We studied the effect of short-term high temperature stress on the survival and development of different stages, adult longevity and fecundity of *Ophraella communa* (Coleoptera: Chrysomelidae), a biological control agent of the invasive plant, the common ragweed, *Ambrosia artemisiifolia* (Asterales: Asteraceae) in the laboratory. The results showed that egg, larval, pupal, and adult survival rates were significantly affected after 2-h short-stress at high temperatures (35 to 47°C) when compared to the 28°C control. With the exceptions of the control and 35°C stress, survival rate of females was significantly higher than that of males after short-stress at any high temperature. Short-term high temperature stress also significantly impacted longevity and fecundity of adult beetles. Except for control, female longevity was significantly longer than male's after short-stress at any high temperature. The survival rates of different stages, and adult longevity and fecundity of the beetle decreased significantly with the increase of short-term stress temperature. Based on the results of the present study, we conclude that the development and population expansion of *O. communa* may be significantly affected when they are exposed to a high temperature stage in a summer day in the areas invaded by common ragweed, in southern China.

Keywords: *Ophraella communa*; short-term high temperature stress; development; fecundity; *Ambrosia artemisiifolia*; population expansion

1. Introduction

It is well known that insects are typical ectotherms andthus are highly sensitive to temperature changes (Hallman and Denlinger 1998). Various insect species have an optimum temperature range for their survival, development, and fecundity (Huffaker, Berryman, and Turchin 1999). Insect's survival, development, and fecundity are affected significantly when the temperature exceeds the optimum range (Huang, Ren, and Musa. 2008). In general, insects are highly vulnerable to high temperature injury (Denlinger and Hallman 1998), thus high temperature is an adverse climatic factor that suppresses population expansion of insects in the field

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(Denlinger and Hallman 1998; Bale et al. 2002). High temperature not only directly accelerates development but it also causes mortality in many insects (Ohgushi and Sawada 1997; Harrington, Woiwod, and Sparks 1999; Cui, Wan, Xie, and Liu 2008; Zhao, Fu, Wan, Guo, and Wang 2009). There are significant differences in the thermotolerance among various insect species (Hodkinson and Bird 2006), thus the differences in their sensitivities to high temperatures are significant (Denlinger and Hallman 1998).

However, negative effects of high temperatures on many insects may be more likely to focus on rates of growth and development, life cycle duration, adult size and fecundity rather than mortality (Denlinger and Hallman 1998; Tammaru 1998; Bird and Hodkinson 1999; Bale et al. 2002; Margraf, Gotthard, and Rahier 2003; Tammaru, Nylin, Ruohomaki, and Gotthard 2004; Hodkinson and Bird 2006; Cui et al. 2008). Since high temperature can accelerate evaporation rate of water from somatic layers of insects, the water metabolism in insects loses balance, and insects may be killed because of water deprivation under extremely high temperature (Denlinger and Hallman 1998; Cui et al. 2008; Zhao et al. 2009). Short-term high temperature can significantly affect individual development, survival, fecundity and physiological metabolism in insects that have been demonstrated in published literature (e.g., Ohgushi and Sawada 1997; Denlinger and Hallman 1998; Harrington et al. 1999; Cui et al. 2008; Zhao et al. 2009). The insects that are highly sensitive to high temperature can be immediately killed under extremely short-term high temperature (Fields 1992; Mourier and Poulsen 2000; Cui et al. 2008; Zhao et al. 2009). Some insect species fail to emerge from pupae after experiencing heat shock, such as *Sarcophaga crassipalpis* and *Drosophila melanogaster* (Mitchell and Lipps 1978; Delinger et al. 1991). In addition, extremely high temperature can induce male insect's sterilities, such as *Drosophila buzzatii*, *Ceratitis capitata*, and *Aedes* mosquitoes (Economopoulos 1996; Vollmer, Sarup, Kærsgaard, Dahlgaard, and Loeschcke 2004), or cause reduced fecundities of female insects such as *Ephestia cautella*, *Plodia interpunctella* and *Agasicles hygrophila* (Arbogast 1981; Cui et al. 2008; Zhao et al. 2009). Thus, populations of insects are often suppressed when they encounter high temperature in the field.

Ophraella communa LeSage (Coleoptera: Chrysomelidae), originally from North America (LeSage 1986; Futuyma 1990), has been identified as a biological control agent of the invasive plant, the common ragweed, *Ambrosia artemisiifolia* L. (Asterales: Asteraceae) (Kiss 2007). It seems to have been accidentally introduced into China and was discovered for the first time in the suburbs of Nanjing City, Jiangsu Province (Meng and Li 2005), where after it has spread rapidly to Jiangxi, Hunan, Hubei, Anhui, Fujian, and Zhejiang provinces in China (Zhou, Guo, Chen, and Wan 2010).

Our previous study showed that an optimum temperature range for development of *O. communa* is 20–30°C, its survival and fecundity dropped rapidly at 32°C, and the neonates were all killed after 24 h at 36°C (Zhou et al. 2010). In addition, our field survey also showed that to some extent, the population of the beetle decreased in the hottest summer days in two recent years (Zhou et al. unpublished data). We hypothesize that the development, survival, and fecundity of *O. communa* are significantly affected even if they survive extremely short-term high temperature. Atmospheric temperature can reach 40°C or above from 13:00 to 15:00 h in summer in southern China (Liu, Zheng, and Wu 2008; Xu, Deng, and Chen 2009;

Anonymous 2010), and *O. communa* is now mainly used for biological control in the areas invaded by common ragweed in southern China. Thus, the 2-h extremely high temperature may significantly affect individual development and population expansion of *O. communa* in summer days in southern China if our above hypothesis is established. To understand the responses of *O. communa* to short-term high temperature, the survival and development of different stages and adult fecundity of the beetle were determined after short-term at different high temperatures in the laboratory.

2. Material and methods

2.1 Host plants

Seedlings of common ragweed originally grown in the nursery, were transplanted individually into 15-cm diameter plastic pots with standardized soil, watered every 4 days and fertilized with a 20% solution of 13:7:15 (N:P:K) twice a month. These potted plants were maintained in an unheated and naturally lighted greenhouse at the Institute of Plant Protection, Hunan Academy of Agricultural Sciences (IPP, HAAS, 25°21’17.81" N, 114°33′40.00" E), and were used for experiments when they reached a height of 40 cm.

2.2 Insects

Ophraella communa pupae were collected on May 10, 2010, from Miluo (28°55′16.64" N, 113°15′51.37" E) in Hunan province in China by picking ragweed leaves with pupae attached. More than 800 pupae were randomly collected from 40 common ragweed plants, 20–25 pupae per plant. All pupae were transported to an insectary at the Institute of Plant Protection, Hunan Academy of Agricultural Sciences, in Changsha City, Hunan Province where they were stored at 28 ± 1°C, a relative humidity of 70 ± 5% and a 14 h L:10 h D photoperiod in a clean transparent plastic box ($19 \times 12 \times 6$ cm) covered with organdy mesh fabric until emergence of adults 5–6 days later. Newly emerged adults were sexed and males and females were held separately on potted ragweed plants, 20 adults per plant. Each plant was isolated in a ventilated, aluminum frame cage ($40 \times 40 \times 60$ cm) under the same insectary conditions as above, and the newly emerged adults were used for experiments.

2.3 Effect of short-term high temperature stress on survival and developmental duration of O. communa eggs

Ophraella communa adults from the stockculture (see section 2.2) were paired and each pair was placed on a potted fresh common ragweed plant in a cage ($60 \times 60 \times 80$ cm) for oviposition. Each potted plant with 200 *O. communa* eggs < 12 h old was placed in a plastic basin (50×30 cm), respectively, which was to absorb water from below. Each plant that had 200 eggs was then allocated randomly and placed in six environmental chambers (PRY-450D, Ningbo Haishu Aifu Experimental Equipment Co. Ltd, Zhejiang, China) at eight temperature regimes (28, 35, 38, 41, 44, 47 ± 1°C) for 2 h, respectively. Irrespective of the temperature, all environmental chambers were set at a relative humidity of 70 ± 5% and a 14 h L:10 h D photoperiod. Among these treatments, the treatment of 28°C was considered as control. Each treatment was repeated successively five times in the same environmental chamber. After the high temperature stress, the potted plants with *O. communa* eggs were transferred to the insectary (see section 2.2). Three days later, eggs were checked and recorded daily until all hatched, and survival rates and developmental durations of eggs were recorded.

2.4 Effect of short-term high temperature stress on survival and developmental duration of O. communa larvae

Ophraella communa adults from the stock culture (see section 2.2) were paired and each pair was placed on a potted fresh common ragweed plant in a cage (60 × 60 × 80 cm) for oviposition. The potted plants with *O. communa* eggs were placed in a plastic basin (50 × 30 cm), which were to absorb water from below, and were placed randomly on the tables in the insectary (see section 2.2). The neonates were kept on the same common ragweed plant when larvae hatched from eggs, and plants with 20 neonates were placed in the six environmental chambers (see section 2.3) for 2 h. After the high temperature stress, the potted plants with larvae were transferred to the insectary (see section 2.2). Each treatment was repeated five times in the same environmental chamber. Larvae were checked daily until pupation, and survival rates and developmental durations of larvae were recorded.

2.5 Effect of short-term high temperature stress on survival and developmental duration of O. communa pupae

Ophraella communa adults from the above culture in the insectary (see section 2.2) were paired and each pair was placed on a potted fresh common ragweed plant in a cage (60 × 60 × 80 cm) for oviposition. The potted plants with *O. communa* eggs were placed in a plastic basin (50 × 30 cm), which were to absorb water from below, and were placed randomly on the tables in the insectary (see section 2.2). The neonates were kept on the same common ragweed's plant until pupation, and plants with 30 newly pupated pupae were placed in the six environmental chambers (see section 2.3) for 2 h. After the high temperature stress, the potted plants with pupae were transferred to the insectary (see section 2.2). Each treatment was repeated five times in the same environmental chamber. Pupae were checked daily until eclosion, and survival rates and developmental durations of pupae were recorded.

2.6 Effect of short-term high temperature stress on survival, longevity and fecundity duration of O. communa adults

Twigs of common ragweed were inserted into plastic bottles (3 × 5 cm, diameter × height) filled with water and with a 0.8 cm diameter hole in the lid to hold the twig. *Ophraella communa* adults from the above culture in the insectary (see section 2.2) were mated and each pair was placed on a ragweed twig. The twigs with beetles were placed in transparent plastic boxes (19 × 12 × 6 cm) covered with organdy mesh fabric. These plastic boxes with *O. communa* adults and common ragweed twigs were placed in the six environmental chambers (see section 2.2) for 2 h. After the high temperature stress, the plastic boxes with adults were transferred to the insectary (see section 2.2). Fresh twigs were changed daily and the eggs of *O. communa* were counted. The observation ended when the females died. A total of 20 pairs were observed for each replication. Each treatment was repeated five times in the same environmental chamber. After the above treatments, adult beetles were transferred to the insectary (see section 2.2) for 24 h, and the number of live adults in each plastic box was recorded. Survival rate, longevity and number of eggs laid per female of *O. communa* adults were then recorded and calculated.

2.7 Statistical analyses

Data were checked for normality and homoscedasticity and, if needed, were arcsine square-root or log-transformed. The developmental periods were firstly transformed by the $\log_{10}(x+1)$, and the survival rates were firstly transformed by arcsine square-root before analysis. A one-way ANOVA was conducted to test for effects of treatments, and Fisher's protected LSD test ($P = 0.05$) was used to separate means when more than two treatments were compared.

3. Results

3.1 Effect of short-term high temperature stress on survival and developmental duration of different immature stages of O. communa

Short-term high temperature stress significantly affected the developmental durations of eggs ($F_{5,24} = 25.84$, $P < 0.0001$), larva ($F_{5,24} = 9.58$, $P < 0.0001$), and pupa ($F_{5,24} = 48.53$, $P < 0.0001$. The developmental durations for pupa shortened significantly along with the increasing stress temperatures. The developmental durations for egg and larva shortened with the increasing stress temperature when temperature was below 38°C, but lengthened with the increase of stress temperature from 41 to 47°C (Table 1).

Short-term high temperature stress also affected the survival rates of egg ($F_{5,24} = 413.90$, $P < 0.0001$), larva ($F_{5,24} = 94.11$, $P < 0.0001$), and pupa

Table 1. Survival rate and duration of various immature stages of *O. communa* after short-term high temperature stress.

	Developmental duration (d)[1]			Survival rate (%)		
Temperature (°C)	Egg	Larva	Pupa	Egg	Larva	Pupa
28	5.8 ± 0.1a	7.8 ± 0.1a	4.6 ± 0.1ab	90.7 ± 1.0a	78.0 ± 3.1a	90.7 ± 1.9a
35	4.9 ± 0.1d	6.63 ± 0.1c	5.0 ± 0.1a	88.5 ± 0.6b	54.0 ± 3.1b	88.7 ± 1.3a
38	4.6 ± 0.1e	6.55 ± 0.2c	4.7 ± 0.1a	80.3 ± 0.7c	42.0 ± 3.9c	78.0 ± 2.7b
41	5.0 ± 0.1cd	6.84 ± 0.2bc	4.3 ± 0.1ab	72.5 ± 0.7d	24.0 ± 3.9d	76.7 ± 1.8b
44	5.2 ± 0.1c	7.21 ± 0.4b	3.9 ± 0.1b	63.2 ± 0.9e	7.3 ± 2.5e	47.3 ± 1.9c
47	5.5 ± 0.1b	–	2.2 ± 0.5c	52.2 ± 0.4f	0.0 ± 0.0e	3.3 ± 2.1d

[1]Mean ± SE. Means within the same column followed by the different letters are significantly different at $P < 0.05$ level according to ANOVA: LSD test. Egg survival rate refers to divide total eggs by hatch eggs, larval survival rate refers to divide total larvae by pupation larvae and pupal survival rate refers to divide total pupae by newly emerged adults after stress treatment at different temperatures 2 h.

($F_{5,24} = 276.65$, $P < 0.0001$) (Table 1). The survival rates of egg, larva and pupa decreased significantly in response to the increasing stress temperature.

3.2 Effect of short-term high temperature stress on survival, longevity and fecundity duration of O. communa adults

Gender ($F_{1,48} = 307.56$, $P < 0.0001$), temperature ($F_{5,48} = 390.24$, $P < 0.0001$), and gender × temperature ($F_{5,48} = 57.51$, $P < 0.0001$) had significant effects on survival rates of adult beetles. Both male ($F_{5,24} = 332.74$, $P < 0.0001$) and female ($F_{5,24} = 86.36$, $P = 0.0009$) beetles varied significantly in survival rates among short-term high temperature stresses. Survival rates of both male and female beetles decreased significantly with increasing stress temperature (Table 2). There was no significant difference between females and males in the survival rates after short-stress at 28°C ($F_{1,8} = 1.00$, $P = 0.3466$) and 35°C ($F_{1,8} = 0.80$, $P = 0.3972$), but survival rates of females were significantly higher than those of males after short-stress at 38°C ($F_{1,8} = 12.25$, $P = 0.0081$), 41°C ($F_{1,8} = 44.10$, $P = 0.0002$), 44°C ($F_{1,8} = 73.92$, $P < 0.0001$), and 47°C ($F_{1,8} = 280.90$, $P < 0.0001$) (Table 2).

Gender ($F_{1,48} = 49.33$, $P < 0.0001$), temperature ($F_{5,48} = 232.43$, $P < 0.0001$), and gender × temperature ($F_{5,48} = 13.63$, $P < 0.0001$) also had significant effects on longevities of adult beetles. The longevities of both male ($F_{5,24} = 170.22$, $P < 0.0001$) and female ($F_{5,24} = 84.66$, $P < 0.0001$) beetles were significantly affected by short-term high temperature stress (Table 2). Longevities of both male and female beetles shortened significantly with increasing stress temperature. There was a significant difference between females and males in the survival rates after short-stress at 28°C ($F_{1,8} = 18.24$, $P < 0.0001$), 35°C ($F_{1,8} = 14.86$, $P = 0.0003$), 38°C ($F_{1,8} = 27.78$, $P < 0.0001$), 41°C ($F_{1,8} = 28.28$, $P < 0.0001$), 44°C ($F_{1,8} = 28.11$, $P < 0.0001$), and 44°C ($F_{1,8} = 9.87$, $P = 0.0026$) (Table 2).

Short-term high temperature stress significantly affected the fecundity of female beetles ($F_{5,24} = 113.06$, $P < 0.0001$). The fecundity of females decreased significantly with the increasing stress temperature (Table 2). *O. communa* females laid most eggs during the early ovipositional periods and showed a significant peak after 2-h

Table 2. Survival rate, longevity and fecundity of adult *O. communa* after short-term high temperature stress.

Temperature (°C)	Longevity (d)[1] Female	Longevity (d)[1] Male	Survival rate (%)[1] Female	Survival rate (%)[1] Male	Fecundity[1] (eggs/female)
28	88.0 ± 1.2a,B	97.8 ± 1.9a,A	100.0 ± 0.0d,A	99.0 ± 1.0e,A	2115.0 ± 49.4a
35	85.7 ± 2.0a,A	76.3 ± 1.4b,B	99.0 ± 1.0cd,A	97.0 ± 2.0de,A	1844.2 ± 45.2b
38	81.0 ± 1.3b,A	71.4 ± 1.2c,B	97.0 ± 1.2cd,A	90.0 ± 1.6d,B	1651.2 ± 58.3c
41	80.9 ± 1.5b,A	69.5 ± 1.5c,B	94.0 ± 1.9c,A	73.0 ± 2.6c,B	1613.7 ± 40.9c
44	62.9 ± 1.3c,A	54.2 ± 1.0d,B	83.0 ± 2.6b,A	48.0 ± 2.6b,B	1130.5 ± 25.5d
47	51.3 ± 2.0d,A	43.6 ± 1.4e,B	57.0 ± 2.6a,A	4.0 ± 1.9a,B	860.3 ± 34.0e

[1]Mean ± SE. Means within the same column followed by the different lower case letters are significantly different from others of the same gender and means within the same row followed by the different upper case letters indicate a significant difference between males and females within a treatment at $P < 0.05$ level according to ANOVA: LSD test. Adult survival rate refers to divide total adults by the live adults that transferred to the insectary of 28 ± 1C for 24 h after 2-h stress treatment.

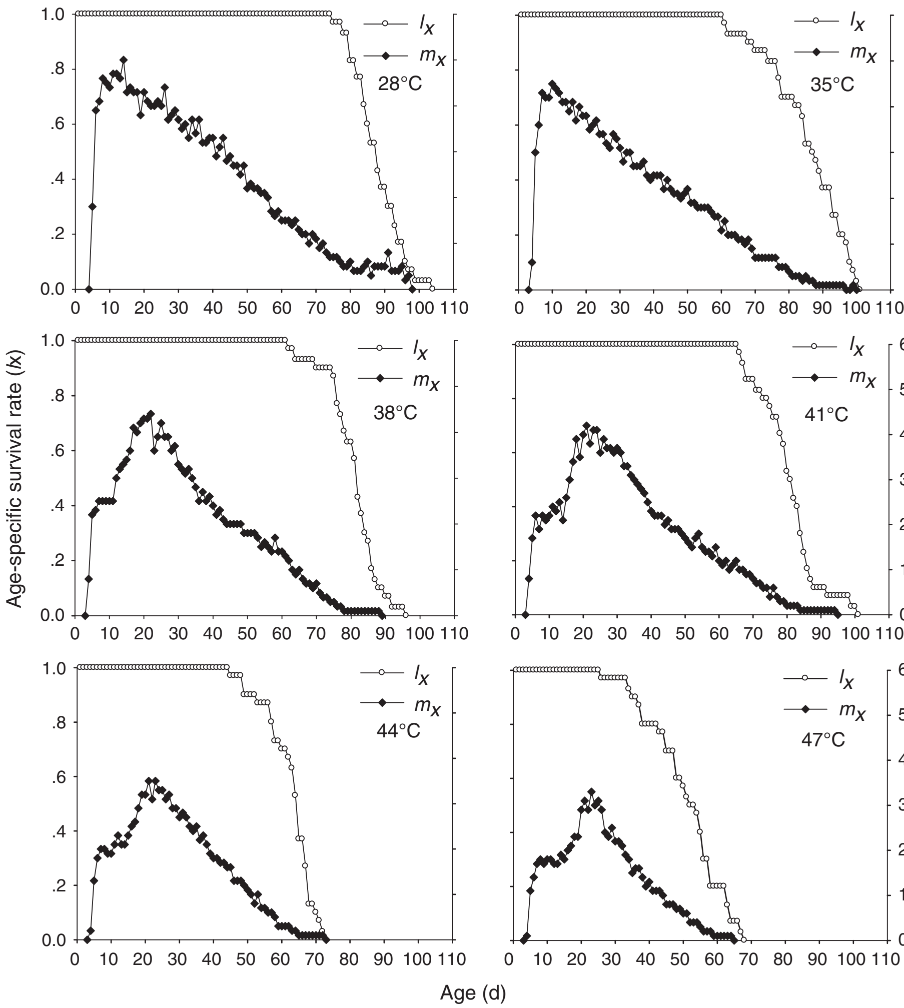

Figure 1. Age-specific survival rate (l_x) and age-specific fecundity (m_x) of female *O. communa* after short-term high-temperature stress.

short-term stress at 28 to 47°C (Figure 1). Almost all females survived up to 75 days at 28°C, but survival rate decreased sharply after 80 days. After 2-h short-term stress at 35, 38, and 41°C, female death occurred between 60 and 65 days. Female death occurred around 45 and 25 days, and all females died within 75 days after 2-h short-term stress at 44 and 47°C (Figure 1).

4. Discussion

Because extremely high temperature performs a complex effect on an insect species, its fitness is probably affected even if it could survive after exposure to heat stress (Scott, Berrigan, and Hoffmann 1997; Rinehart, Yocum, and Denlinger 2000; Cui et al. 2008; Zhao et al. 2009). For example, adult survival rates of both *Trialeurodes* *vaporariorum* and *Bemisia tabaci* biotype B decreased significantly when they were exposed at 41°C or higher for *B. tabaci* or 39°C or higher for *T. vaporariorum*, and the fecundity of *T. vaporariorum* females declined with the increase of heat shock temperature, and only a few eggs were laid at 43°C (Cui et al. 2008). Both longevities and fecundities of *Agasicles hygrophila* adults decreased significantly with the increase of 1 h stress temperature (Zhao et al. 2009). The results of the present study showed that the survival rates of egg, larva, pupa and adult of *O. communa* decreased significantly with the increase of short-term stress temperature. In addition, the longevity and fecundity of adult beetles also significantly decreased with increasing short-term stress temperature. Our results are therefore in accordance with expectations and previous studies (e.g., Scott et al. 1997; Rinehart et al. 2000; Cui et al., 2008; Zhao et al. 2009). Interestingly, we found that the developmental durations for eggs and larvae lengthened with the increasing short-term stress temperature when the temperature exceeded 41°C. This differs from the previous findings that the developmental durations of insects were shortened at high temperature (e.g., Ohgushi and Sawada 1997; Scott et al. 1997; Harrington et al. 1999; Rinehart et al. 2000; Cui et al. 2008; Zhao et al. 2009).

In heat-resisting insect species, even if the development and survival of their immature stages were significantly impacted by heat stress, fecundity was still not significantly different when their adults were heat-shocked at various high temperatures such as *B. tabaci* (Cui et al. 2008). Thus, we conclude that *O. communa* belongs to a heat-sensitive insect species. We found that with the exceptions of the control and 35°C stress, survival rate of females was significantly higher than that of males after short-stress at any high temperature. Female's longevity was, except for control, significantly longer than male's after short-stress at any high temperature. This may be helpful to the re-establishment and re-expansion of *O. communa* population after experiencing an extremely high temperature in the field.

Global climate warming, commonly accepted as a reality by both scientists and the general public (Walther et al. 2002; Helmuth, Kingsolver, and Carrington 2005; Parmesan 2006; Musolin, Tougou, and Fujisaki 2010), can be often translated in more frequent and stronger heat waves, especially during summer months (Tripathee 2008; Anonymous 2010). Indeed, in recent years, an abnormal climate has been reported repeatedly that heat wave effect induces extremely short-term high temperatures in a summer day in southern China (Liu et al. 2008; Xu et al. 2009; Anonymous 2010). The results of the present study imply that the development, fecundity and population expansion of *O. communa* may be significantly affected when experiencing a high temperature stage in a summer day in the areas invaded by common ragweed, in southern China.

In general, physiological metabolisms in insects vary significantly when they are heat-shocked at extremely high temperature in order to defend and avoid high temperature injury (Denlinger and Hallman 1998; Musolin 2007; Bale et al. 2002). Previous studies suggested that heat shock protein 70 (hsp70) family appears to be the most prominent contributor to thermotolerance in insects (Denlinger and Hallman 1998), since hsp70 is the protein that responds most dramatically to heat shock (Velazquez, Sonoda, Bugaisky, and Lindquist 1983). In addition, classic cryoprotectants such as glycerol (Henle and Warters 1982), glycogen (Denlinger and Hallman 1998), sorbitol (Wolfe, Hendrix, and Salvucci 1998; Salvucci, Stecher, and Henneberry 2000), and lipids (Denlinger and Hallman 1998) are reported to protect cultured cells against high temperature stress. Thus, the physiological mechanism of insect's thermotolerance can be revealed by the synthesis of heat shock proteins and accumulation of classic cryoprotectants in insects.

We only observed that the biological indices (i.e., survival, development, and fecundity) of *O. communa* were impacted after short-term high temperature stress in this study. However, the physiological responses of *O. communa* (especially in adults) to short-term high temperature stress have yet to be explored, and the expression of heat shock proteins and levels of classic cryoprotectants in *O. communa* may be considered as the focus field in our further study. Extremely short-term high temperature stress is the thermal injury caused by a sudden increase in temperature (Denlinger and Hallman 1998). But, this form of injury can be dramatically reduced when the organism is first pretreated at an intermediately high temperature prior to exposure to extremely high temperature (Mitchell, Moller, Petersen, and Lipps-Sarmiento 1979), which is often called heat acclimation. Increased thermotolerance of insects is often attained by long-term acclimation or rapid heat hardening (Denlinger and Hallman 1998). This offers useful information that the high heat-resistant population of *O. communa* may be attained by long-term acclimation or rapid heat hardening, which contributes to increase of the control potential of the beetle on common ragweed in the field. Based on the results of present study, the difference in thermotolerance between the field-collected insects and those reared at constant temperatures may be our follow up study.

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