Quan Yudong (Orcid ID: 0000-0002-5896-4916)

Original Article

Impact of heat waves on egg survival and biological performance across life stages in the Asian corn borer

Yudong Quan[1], Charles E. Mason[2], Kanglai He[1]*, Zhenying Wang[1] & Hongyi Wei[3]

[1]State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, No.2, West Yuanmingyuan Road, Haidian District, Beijing 100193, China, [2]Department of Entomology and Wildlife Ecology, University of Delaware, 531 S College Ave Rm 250, Newark, DE 19716-2160, USA, and [3]College of Agronomy, Jiangxi Agricultural University, Nanchang 330045, Jiangxi Province, China

***Correspondence:** Kanglai He, State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, No.2, West Yuanmingyuan Road, Haidian District, Beijing 100193, China. E-mail: hekanglai@caas.cn, klhe@ippcaas.cn

Short title: SUBSEQUENT EFFECT OF HEAT SHOCK AT THE EGG PERIOD

Keywords: developmental time, fecundity, heat shock, life table, *Ostrinia furnacalis*, sex ratio, Lepidoptera, Crambidae, maize pest, heat treatment

Accepted: 27 April 2022

Accepted Manuscript
Version of record at: https://doi.org/10.1111/eea.13262

Abstract

One of the many extreme events as a result of climate change is the frequent appearance of extraordinarily daily high temperatures that can directly drive an insect's adaptive response. Insects have complex life cycles that may uncouple temperature's effects in one stage from the physiology in the next. In this study we focused on the Asian corn borer (ACB), *Ostrinia furnacalis* (Guenée) (Lepidoptera: Crambidae), one of the most important pests of maize (corn) in Asia, investigated the consequences of eggs exposed to ecologically relevant heat shock regimes, simulating heat waves at extreme high temperature. This consisted of five 90-min heat treatments separated by two degrees that ranged from 37 to 45 °C for three consecutive days compared to a constant temperature of 25 °C. Temperature that triggered mortality was between 39 and 41 °C. Egg hatching significantly declined when temperature was 41 °C or higher. There was no egg hatching at 45 °C. Developmental times were significantly prolonged and the larval growth rate became slower in treatments of 41 and 43 °C. There were no significant differences in pupal mass, fecundity, and sex ratio among treatments. Life table parameters showed significant adverse effects at treatments of 41 and 43 °C. Depending on the fitness response of the ACB, environmental heat waves can be classified into three categories based on temperature criteria, i.e., adaptable (35–39 °C), critical (39–45 °C), and fatal (≥45 °C). The findings of the present study will serve as an important reference for forecasting the population dynamics of the ACB.

Abbreviated abstract

Asian corn borer (ACB), *Ostrinia furnacalis* (Lepidoptera: Crambidae), mostly lay egg-masses on the underside of maize leaves. Immobile eggs are unable to avoid heat-shock during heat waves. We investigated the consequences of eggs exposed to heat-shocks, simulating heat waves at extreme high temperature. Based on ACB's fitness response, heat waves can be classified into adaptable (35–39 °C), critical (39–45 °C), and fatal (>45 °C). These findings will serve as an important reference for forecasting ACB population dynamics.

Graphic for Table of Contents

Graphical abstract.pdf

Introduction

Recent research concerning climate change has demonstrated that the average global temperatures have increased. Along with this, the frequency of extremely high temperature events has increased by 40% around the world over the past 60 years (Donat & Alexander, 2012). Furthermore, heat waves associated with climate change are predicted to increase in duration, frequency, and/or intensity with a 90–99% probability (IPCC, 2014). Through natural selection, adaptation to heat stress is often a strong evolutionary factor leading to the spread and successful establishment of an insect species (Bijlsma & Loeschcke, 2000; Willmer et al., 2000; Kang et al., 2009), although the functional temperature range as an environmental context for physiological activity is rarely within temperatures of 40–50 °C (Heinrich, 1981). Pauli et al. (1992) have defined heat shock responses as major alterations in genetic activity in every organism after transient exposure to abnormally high temperatures. Thus, heat-shock response could be considered as a major source of alternations in fitness in a species after exposure to extreme high temperatures (i.e., ranging from 37–45 °C) for short time periods during a heat wave scenario. In insects, temperature-driven plasticity is ubiquitous (Ananthakrishnan & Whitman, 2005; Whitman & Ananthakrishnan, 2009), and the effects are significant. Therefore, extremely high environmental temperature may result in substantial challenges for insect reproduction and subsequent survival (Clarke, 2003). So, the heat waves that create more frequent events of heat stress will inevitably impact the various life stages of insects in the field. In order to establish whether this will significantly affect the development or other biological characteristics of insects, it is important to understand the response of insects to heat waves, especially for agricultural pests.

Development and reproduction in insects with holometamorphosis are essential for survival, which are also relevant to pest control in agriculture. A perfect overlap between insect development and key crop growing is not expected because of the many stages in which the insects can feed. However, a small change to adapt to higher temperature will potentially impact an insect's growth and life cycle stage (Bale et al., 2002; Ananthakrishnan & Whitman, 2005; Parmesan, 2006; Wang et al., 2009a,b; Zhou et al., 2018), and may induce compensatory responses in subsequent life stages (Metcalfe & Monaghan, 2001). For the major agricultural pests of lepidopteran insects, the holometamorphosis life cycle is divided into multiple life stages culminating in metamorphosis. The larva period of Lepidoptera is of major concern because this life stage does the feeding that results in damage to the crop. This leads to forced pesticide use and various other tactics to manage the pest. Insects are sensitive

to thermal stress in all the periods of development, which can result in changes in behavioral and physiological responses. Most of the mobile larvae and adults of Lepidoptera are more likely to seek protection from the elements, or enter diapause or another form of dormancy in order to pull through the extreme thermal stress. Because of immobility, their eggs and pupae can only improve physiologically against the stress. Even worse, the eggs are mostly laid on the crops where they are exposed to the elements at the surface. Egg temperature in animals can affect subsequent performance across life stages, including growth rate (Hare et al., 2009), morphology (Kingsolver et al., 2011), muscle phenotype (Macqueen et al., 2008), behavior (Flores et al., 1994), fecundity (Callebaut, 1991), and even immune function (Ardia et al., 2010). Although insects may benefit from compensatory growth after a poor egg environment (Simpson & Simpson, 1990; Yang & Joern, 1994; Taylor et al., 1998; Woods, 1999), there hardly have been systematic studies on the effect of the extreme thermal environment on development and reproduction when exposure occurs during the egg period.

Asian corn borer (ACB), *Ostrinia furnacalis* (Gueneé) (Lepidoptera: Crambidae), is the most important insect pest of maize (corn) in Asia and some Pacific islands (Schreiner et al, 1990; Zhou, 1995; Goto et al. 2001; Nonci, 2004; Afidchao et al., 2013; Quan et al., 2015). It occurs in various agro-climatic regions (Xie et al., 2015). It has 1–7 generations extending from cool-temperate regions to subtropical areas and can have continuous overlapping generations in tropical areas (Nafus & Schreiner, 1991; Zhou et al., 1995). The optimum temperature for growth and development ranges from 20 to 32 °C (He et al., 2018). The ACB normally deposits the majority of its egg masses on the basal two-thirds of the leaf blade near the midrib on the underside of maize leaves, whereas a few egg masses are laid on the leaf sheath and upper surface of leaf blades (Zhou et al., 1995). First instars of ACB usually move directly into the whorl for shelter and food. They establish in between the unexpanded leaves until tasseling, the later instars usually move and burrow into the leaf axil, leaf sheath, and stalk. Pupation takes place inside the tunnels of the host (Nafus & Schreiner, 1991; Zhou et al., 1995). The moths normally inhabit in aggregation sites where the habitats are usually grassy areas or dense vegetation in crop canopies (such as wheat and soybean) adjacent to maize fields. The most suitable aggregation sites are along waterways and drainage areas with sufficient moisture to produce dense vegetation. Female moths normally fly from aggregation sites to the maize field to lay eggs at night. Therefore, the immobile egg stage, which is without parental protection and lacking the ability to avoid extreme high temperature, is the most critical life stage when subjected to heat-shock during an episode of extreme high temperature. So, acclimation is the only way to adapt to this change through its own

Accepted Manuscript
Version of record at: https://doi.org/10.1111/eea.13262

perception and regulation, or death will occur (Bowler, 2005). The question is what post-exposure features of the insect's life cycle are directly adaptive responses to extreme high temperatures ranging from 37 to 45 °C for a transient 90-min period when exposed during the egg stage?

Materials and methods

Insect stock

Ostrinia furnacalis has been reared for several generations using an artificial diet and techniques described by Zhou et al. (1995). In brief, larvae were reared with 16 h photophase when the lights came on in the morning (06:00 hours) at 25 + 0.5 °C and 75% r.h. Pupae were transferred into mating and ovipositing cages, which were maintained at 25 + 0.5 °C and 80% r.h. with 8 h scotophase. In the morning, the fresh egg masses were collected and used for this study.

Heat shock treatment

The thermal regimes were set up at 37, 39, 41, 43, and 45 °C based on historical records of day temperatures in northern China where the maximum day temperature is normally 35–37 °C in the summer, and the extreme high temperature during the day could well exceed 40 °C (Ju et al., 2014). The high temperatures often occur between 12:00 and 16:00 hours and are preceded by a gradual increase in temperature from sunrise to 14:00 hours, and the hold time of maximum temperature is about 1–2 h (Ju et al., 2011) corresponding with 90 min exposure in the present study.

For each experiment, newly laid egg masses (<12 h old) of ACB were randomly divided into six treatment groups with 200–400 egg masses each, which were placed in a transparent plastic zip-lock bag for each group. One group that served as the control was incubated in the insectary at 25 ± 0.5 °C, 75% r.h., and L16:D8 photoperiod until hatching. The other five groups were heat-shock treated for 90 min during 12:00–16:00 every day for three consecutive days in temperature-regulated chambers (RXZ-430B, Ningbo, China) at 37 ± 0.5, 39 ± 0.5, 41 ± 0.5, 43 ± 0.5 and 45 ± 0.5 °C, with 50 ± 10% r.h., respectively. Each temperature-regulated chamber was warmed up to the setting temperature at least 60 min before the treatment started. Once the heat shock treatment was accomplished each day, the egg masses were immediately transferred into the insectary and held under the same conditions as the control. The egg treatment experiment as described was replicated 3×.

Insect rearing trials

Individual rearing

Egg hatching time and number of hatched eggs were recorded by observation under a stereomicroscope for at least 60 egg masses in each treatment group. The setup for life-history studies was initiated by selecting 90 neonates from 30 egg masses per treatment group. Each individual was carefully transferred into a 15-ml centrifuge tube filled with 5 g of artificial diet (Zhou et al., 1995) at the bottom. The tubes were sealed with a piece of sterilized cotton and appropriately labelled. These were subsequently maintained in the insectary under the same rearing conditions described in the previous experiment for the egg mass controls. Once the larvae pupated, they were carefully weighed and transferred to a new tube (15 ml) where they continued developing to eclosion. Numbers of eclosed male and female moths were recorded. Male and female pairs were placed in a new tube (30 ml), and fed 10% hydromel (Zhou et al., 1995) (honey:water = 1:10 wt/wt) through a new sterilized cotton ball every day.

Larval duration was recorded as the period from hatching until pupation and pupal period was recorded as the time from pupa appearance to adult emergence. The sex ratio was assessed by examining external genitalia features for both pupae and adults. Time in adult stage was determined as days from eclosion to death. Insects that reached the adult stage were classified as completing the life cycle.

Mass rearing

Besides individual rearing of the larvae, the left-over larvae from the hatched egg experiment were reared in transparent 600-ml plastic bottles, where the density was about 80–100 insects per bottle for each treatment. When larvae developed to pupae, sex was determined by the genitalia. Ten pairs of male and female pupae, where individuals of each pair were of the same age (a female pupa weighed 70–80 mg, a male 50–60 mg), were placed in an oviposition cage (7.5 × 7.5 × 10 cm, all 16-mesh hardware aluminum-screen) supplied with a new 10% hydromel sterilized cotton ball every day. Caged pairs were maintained in the adult insectary with 25 ± 0.5 °C, 80–90% r.h., and L16:D8 photoperiod. Subsequent to moth emergence, a piece of wax paper that served as an oviposition substrate was placed on the top mesh surface of the cage, whereupon wax paper with or without egg masses was collected and refreshed daily. Five cages were assigned for each heat shock treatment that had adult survivors.

Experimental design and data analysis

Population features (life table parameters) were calculated according to the age-specific life table method (Birch, 1948). Net reproductive rate was computed as: $R_0 = \sum l_x m_x$, where l_x is the probability of an individual living to age x and m_x was the average number of offspring produced by females of age x. Average generation time (t) was the average time in days between egg hatch to next generation of offspring born. Innate capacity for increase was $r_m = \ln R_0/t$. Finite rate of increase was $\lambda = e^{r_m}$. Population parameters were calculated as reported by Maia et al. (2000). Then we used Kruskal-Wallis (H) and Mann-Whitney (U) to test for significant differences.

Larval developmental rate (R) was calculated using equation: $R = (\ln P - \ln L)/t_l \times 100\%$ (Gotthard et al., 1994), where P is the pupal mass, L the newly hatched larval weight, and t_l the time in the larval stage. One hundred neonates as a group were weighed and three groups were weighed to determine L, which resulted in an average weight of a larva of 0.6 ± 0.1 mg.

This study was a randomized complete block design conducted as a single factorial experiment and repeated (block) 3×. All data were subjected to homogeneous variance tests and analyzed using the statistical package software IBM SPSS Statistics v.20.0 (IBM, Armonk, NY, USA). Effects of temperature on development time were assessed using a Kaplan-Meier analysis (log-rank test). QQ-plots were used to test the assumption of normally distributed data and the results of Kolmogorov-Smirnov and Shapiro-Wilk tests were applied. One-way ANOVA was used to test for differences in pupal weights by Fisher's protected least significant difference (LSD) test ($\alpha = 0.05$). If the data did not fit a normal distribution, we used nonparametric Kruskal-Wallis (H) and Mann-Whitney (U) tests. The proportion of eclosion, hatching rate, and survival rate were analyzed using χ^2 tests.

Results

Survival to hatching

The effect of heat shock temperatures on egg hatching rate was different among the six treatments ($\chi^2 = 180.56$, d.f. = 4, $P<0.001$). More than 90.9% of eggs successfully hatched at 39 °C and lower. There were no significant differences among 25, 37, and 39 °C ($\chi^2 = 0.83$, d.f. = 2, $P = 0.66$). At higher temperatures, egg hatching rates significantly declined by 28.3 and 39.2% for 41 and 43 °C, respectively. No eggs hatched at 45 °C (Figure 1A).

When those neonate larvae from each of the treatments were reared on the diet, there

were significant differences in the proportion of larvae completing their life cycles (Figure 1B). The survival rates at 37 and 39 °C were not significantly different from the control at 25 °C. In contrast, the survival rate was significantly decreased by around 10% at 41 and 43 °C (Figure 1B).

Developmental time

There was no significant impact on time for completion of egg development for all heat shock treatments. Although none of the eggs at 45 °C hatched, the larvae within them appeared fully developed. Therefore, it was judged that all egg masses completed development in 4 days in all treatments. However, larval, pupal, and adult development times varied significantly among the treatments (excluding 45 °C). With increasing treatment temperatures, the trend for development time gradually decreased (albeit not significantly) from 25 to 39 °C. Then at the two treatment temperatures above 39 °C there was an increase in development time (female: $F_{4,167} = 7.691$; male: $F_{4,172} = 6.825$, both $P<0.001$) (Figure 2A). Pupal developmental time was somewhat variable across the heat shock treatment temperatures. Female pupal development was different among the treatments ($F_{4,163} = 2.667$, $P = 0.034$), particularly it increased at 43 °C compared with 25 or 39 °C ($F_{4,163} = 2.506$, $P = 0.032$), but was not different for male pupal development ($F_{4,171} = 1.542$, $P = 0.19$) (Figure 2B). Although both females and males had the longest times in the adult stage at 39 °C, there were no significant difference among treatments (female: $F_{4,148} = 1.496$, $P = 0.21$; male: $F_{4,164} = 0.206$, $P = 0.94$) (Figure 2C). The lifespan of ACB had a response profile very similar to that of the time of development for the larvae across all heat shock treatments (Figures 2A and 2D).

Larval growth rate, pupal weight and fecundity

Larval growth rate showed significant variation (female: $\chi^2 = 14.47$, $P = 0.002$; male: $\chi^2 = 20.78$, $P<0.001$, both d.f. = 4) among heat shock treatments (Figure 3A). Both female and male larval growth rates followed similar trends across the five treatment temperatures (Figure 3A). Larval growth rates increased as the heat shock treatment temperature increased up to 39 °C, but not significantly (Figure 3A). However, there was a significant decline in larval growth rate at the two heat treatments above 39 °C (Figure 3A). Larval growth rates did not change significantly in females and males (female: $44.5 \pm 3.1\%$ day^{-1}; male: $45.4 \pm 2.6\%$ day^{-1}).

Female pupae weights tended to increase as the temperature of heat shock treatment increased (Figure 3B), but there was no difference among the treatments ($F_{2,166} = 0.854$, $P =$

0.49). Male pupal weights were relatively consistent across heat shock treatments, except at 39 °C, when they were heavier compared to the others ($F_{2,172} = 3.152$, $P = 0.016$). There was no difference in the fecundity ($F_{4,10} = 0.133$, $P = 0.25$), nor in the female-to-male sex ratio ($F_{4,10} = 0.562$, $P = 0.20$) among the treatments (Figure 3C and 3D).

The time period for development from egg to adult eclosion peaked at 27–28 days for males at 25, 37, 39, and 41 °C and for females the peak at these temperature treatments was 28–29 days (Figure 4). The 43 °C treatment had the longest peak time for both males and females at 29 days.

Life table parameters

Survival analysis showed differences among life table parameters following heat shock temperature treatments in the egg stage (R_0, $F_{4,10} = 5.332$, $P = 0.022$; T, $F_{4,10} = 8.238$, $P = 0.004$; r_m, $F_{4,10} = 12.485$, $P = 0.014$; and λ, $F_{4,10} = 12.413$, $P = 0.014$) (Table 1). In general, the effect of heat shock treatments on eggs showed similar trends, i.e., R_0, r_m, and λ slowly increased as temperature of the heat shock treatment increased from 25 to 39 °C and the average generation time (t) decreased, but they were not significantly different among those treatments. However, at 41 and 43 °C, these were significantly different for all four life table parameters (Table 1).

Discussion

In the context of climate warming, the frequency and intensity of heat waves have considerably increased since the late 20th century (Xia et al., 2016). Obviously, appearance of heat waves has become a new normal characteristic of extreme weather, in association with the changing World's climate. For many organisms, it is considered that prior experience of a novel environment can give rise to a performance advantage (Krebs & Loeschcke, 1994; Gray, 2013; Sambucetti et al., 2013), and should lead to survival adaptation or to death depending on how it is driven by the stress (Bowler, 2005). In this study, ACB egg masses exposed to various intensities of heat shock regimes resulted in different levels of success of insect survival, development, and reproduction. Survival to hatching was not significantly different from the heat shock treatments of 37 or 39 °C vs. the control of 25 °C. However, a vital effect in survival and cross-stage consequences was indicated when the heat-shock regime rose above 39 °C. Egg hatching rates significantly declined by 28.3 and 39.2% along with the treatment temperature rising up to 41 and 43 °C, respectively, suggesting a critical

heat shock point between 39 and 41 °C. There was no egg that hatched to a larva at 45 °C (Fig.1 A). This revealed that the upper limit of their tolerance to heatwave intensity was below 45 °C.

The fact that ACB eggs could not endure the 90 min heat-shock treatment of 45 °C, suggests that an extreme heat wave of 45 °C or higher in summer even for a short period will be profoundly fatal to embryonic development and will definitely affect the ACB in getting through the summer. Previous findings indicate that ACB survival to hatching decreased significantly by ca. 13% with long exposure (6 h) to 39 °C compared to 37 °C but the survival was not significantly different from the survival at 27 and 35 °C for ACB (Quan et al., 2015). Similar results are demonstrated in cotton pests *Helicoverpa armigera* Hübner and *Helicoverpa punctigera* (Wallengren) (Qayyum & Zalucki, 1987). *Manduca sexta* (L.) eggs were able to stay alive at a 2 h exposure of 43 °C (Potter et al., 2009). These studies suggest that tolerance to high extreme temperature is species specific for certain insects in terms of maximum daytime temperature and for length of time it persists. In our study, it was concluded that the optimum survival rate of ACB eggs when exposed to a short period of heat shock (90 min) is around 39 °C. At higher heat shock temperatures, egg survival falls off precipitously.

Biological characteristics of an insect are evolved to adapt to the changing environment, with a certain rationality and stability (Southwood, 1977). Andrewartha & Birch (1954) suggested the adverse impact of previous exposure to high temperature may appear at some later 'critical' stage, inducing high mortality at that stage. However, cross-stage fitness consequences of ecologically relevant egg temperatures (including heat shock of 2 h exposure to 43 °C) would disappear rapidly during subsequent life stages (Potter et al., 2011). In our study, the consequences of egg heat shocks depended on the intensities of heat shock regimes. Heat shock regimes of 35, 37, and 39 °C did not significantly affect the biological parameters measured in larval, pupal, and adult stages. According to the life table parameters we studied, population features performed higher as the temperature increased up to 39 °C, indicating that the optimal constant temperature for egg survival is >25 °C. In contrast, heat shock regimes of 41 and 43 °C induced high mortality of ca. 13% at the larval stage. In addition, life table parameters were adversely affected for the survivors at 41 and 43 °C, which suggested a heat tolerance-related fitness cost for ACB in nature. This is in accordance with the temperature criteria up to and including 39 °C favoring fitness and temperatures higher than that imparting fitness costs.

The tolerance to heat shock was enhanced by heat hardening in sycamore lace bug,

Corythucha ciliata (Say) (Ju et al., 2011). Frequent extreme temperature is a non-continuous and strong pressure which has a strong influence on population homeostasis (Kultz, 2005). Sublethal high temperatures may lead to alterations in morphology, development, longevity, phenology, fertility, and fecundity. Exposure to high temperatures resulted in decline of longevity, oviposition period, and fecundity of *H. armigera* (Mironidis & Savopoulou-Soultani, 2010). The impact of heat shock continued into the next generation in two whiteflies, *Bemisia tabaci* (Gennadius) and *Trialeurodes vaporariorum* (Westwood) (Cui et al., 2008). Results from a previous study with a single extreme temperature treatment (42 °C) for 1–3 h on eggs of ACB showed significant impact, i.e., low egg hatching, declined larval survival, and slower larval development (Zhou et al., 2018). In our study, ACB directly responded to critical heat shocks to eggs above 39 °C with slower larval development and growth. Conversely, larval development and growth rate increased with increasing temperatures of heat shocks (35–39 °C) applied to the eggs. The cost of heat tolerance (>39 °C) is possibly mediated by physiological factors such as heat shock proteins (González-Tokman et al., 2020). This could be considered the direct physiological response to high temperature extreme of climate change events. Selection for heat resistance to test the adaptive evolution of upper temperature tolerance as a consequence of direct effects of natural selection needs to be done by empirical experiments.

Meteorologically, heat waves have been defined variously based on the indices of high temperature extremes such as intensity and/or duration (Jones et al., 1999; Robinson, 2001; Yan et al., 2002; Meehl & Tebaldi, 2004; Ding et al., 2010; Perkins & Alexander, 2013; Xia et al., 2016). Generally, the criteria of heat waves are defined by the China Meteorological Administration: a high temperature extreme is 35 °C or higher and lasts 3 days or more (Xu et al., 2009; Zhang et al., 2005, 2008; Ding et al., 2010). Therefore, three categories of heat waves could be applied, with criteria of temperature ranging from 35–39 °C, >39 °C but <45 °C, and ≥45 °C as well as lasting 3 days or more, according to their impact on ACB eggs, i.e., adapted ($35 \leq T \leq 39$ °C), critical ($39 < T < 45$ °C), and fatal (≥ 45 °C) heat waves. Historically, the adapted heat waves (≤ 39 °C) are common in most areas of China (Xu et al., 2003; Chen & Fan, 2007; Ding et al., 2010, 2015). Therefore, as a characteristic of climate warming, high temperature extremes (heat waves) are commonly favoring the ACB population. Although there are hardly fatal heat waves (≥45 °C) in the maize producing areas of China in the historical records, the critical heat waves (>39 °C) have often been observed (Chen & Fan, 2007; Xu et al., 2003, 2009). In 2014, there was a period of 10 days with the temperatures elevated from 35 to 43.9 °C in China and there is an increasing trend for

something of this nature to continue in the future. Extreme heat of this nature will certainly affect the ACB population, particularly if the heat wave is higher than 39 °C. The anticipated results will decrease the population, and slow larval development and growth. In the field, daily temperature fluctuates and the peak day temperature is normally reached via a gradual increase from sunrise. In this study, we used heat shock to simulate heat waves. However, it should be kept in mind that the sudden change in temperature rather than a gradual increase might have a different impact on the measured factors.

Acknowledgments

This research was funded by the National Key R&D Program of China (2017YFD0201802).

References

Afidchao MM, Musters CJ & de Snoo GR (2013) Asian corn borer (ACB) and non-ACB pests in GMcorn (*Zea mays* L.) in the Philippines. Pest Management Science 69: 792–801.

Ananthakrishnan TN & Whitman D (2005) Insect Phenotypic Plasticity: Diversity of Responses. Science Publishers, Enfield, NH, USA.

Andrewartha HG & Birch LC (1954) The Distribution and Abundance of Animals. University of Chicago Press, Chicago, IL, USA.

Ardia DR, Pérez JH & Clotfelter ED (2010) Experimental cooling during incubation leads to reduced innate immunity and body condition in nestling tree swallows. Proceedings of the Royal Society B 277: 1881-1888.

Bale JS, Masters GJ, Hodkinson ID, Awmak C, Bezemer TM et al. (2002) Herbivory in global climate change research: directeffects of rising temperature on insect herbivores. Global Change Biology 8: 1-16.

Bijlsma R & Loeschcke V (2000) Environmental stress, adaptation and evolution: an overview. Journal of Evolutionary Biology 18: 744-749.

Bowler K (2005) Acclimation, heat shock and hardening. Journal of Thermal Biology 30: 125-130.

Callebaut M (1991) Influence of daily cyclical variations of embryonic incubation temperature on ovarian morphology in the adult Japanese quail. European Archives of Biology 102: 171-173.

Chen HB & Fan XH (2007) Some extreme events of weather, climate and related phenomena

in 2006. Climatic Environment Research 9: 218-223.

Clarke A (2003) Costs and consequences of evolutionary temperature adaptation. Trends in Ecology and Evolution 18: 573-581.

Cui XH, Wan FH, Xie M & Liu TX (2008) Effects of heat shock on survival and reproduction of two whitefly species, *Trialeurodes vaporariorum* and *Bemisia tabaci biotype* B. Journal of Insect Science 8: 24.

Ding T, Qian WH & Yan ZW (2010) Changes in hot days and heat waves in China during 1961-2007. International Journal of Climatology 30: 1452-1462.

Ding T & Ke ZJ (2015) Characteristics and changes of regional wet and dry heat wave events in China during 1960-2013. Theoretical and Applied Climatology 122: 651-665.

Donat MG & Alexander LV (2012) The shifting probability distribution of global daytime and night-time temperatures. Geophysical Research Letters 39: L14707.

Flores D, Tousignant A & Crews D (1994) Incubation temperature affects the behavior of adult leopard geckos (*Eublepharis macularius*). Physiology & Behavior 55: 1067-1072.

González-Tokman D, Córdoba-Aguilar N, Dáttilo W, Lira-Noriega A, Sánchez-Guillén RA & Villalobos F (2020) Insect responses to heat: physiological mechanisms, evolution and ecological implications in a warming world. Biological Reviews 95: 802-821.

Gotthard K, Nylin S & Wiklund C (1994) Adaptive variation in growth rate: life history costs and consequences in the speckled wood butterfly, *Pararge aegeria*. Oecologia 99: 281-289.

Goto M, Sekine Y, Outa H, Hujikura M & Suzuki K (2001) Relationships between cold hardiness and diapause, and between glycerol and free amino acid contents in overwintering larvae of the oriental corn borer, *Ostrinia furnacalis*. Journal of Insect Physiology 47: 157-165.

Gray EM (2013) Thermal acclimation in a complex life cycle: the effects of larval and adult thermal conditions on metabolic rate and heat resistance in *Culex pipiens* (Diptera: Culicidae). Journal of Insect Physiology 59: 1001-1007.

Hare KM, Longson CG, Pledger S, Daugherty CH & Beaupre SJ (2009) Size, growth, and survival are reduced at cool incubation temperatures in the temperate lizard *Oligosoma suteri* (Lacertilia: Scincidae). Copeia 2004: 383-390.

He HM, Xiao L, Chen QW & Xue FS (2018) A life-history trait of the Asian corn borer, *Ostrinia furnacalis* (Lepidoptera: Pyralidae) – positive correlation between body weight and temperature. Acta Entomologica Sinica 61: 340-347. (In Chinese with English abstract)

Heinrich B (1981) Ecological and evolutionary perspectives. Insect Thermoregulation (ed. by B Heinrich), pp. 235-302. Wiley, New York, NY, USA.

IPCC (2014) Summary for Policy Makers. Cambridge University Press, Cambridge, UK.

Jones PD, Horton EB, Folland CK, Hulme M, Parker DE & Basnett TA (1999) The use of indices to identify changes in climatic extremes. Climatic Change 42: 131-149.

Ju RT, Chen GB, Wang F & Li B (2011) Effects of heat shock, heat exposure pattern, and heat hardening on survival of the sycamore lace bug, *Corythucha ciliata*. Entomologia Experimentalis et Applicata 141: 168-177.

Ju RT, Gao L, Zhou XH & Li B (2014) Physiological responses of *Corythucha ciliata* adults to high temperatures under laboratory and field conditions. Journal of Thermal Biology 45: 15-21.

Kang L, Chen B, Wei JN & Liu TX (2009) Roles of thermal adaptation and chemical ecology in *Liriomyza* distribution and control. Annual Review of Entomology 54: 127-145.

Kingsolver JG, Woods HA, Buckley LB, Potter KA, MacLean HJ & Higgins JK (2011) Complex life cycles and the responses of insects to climate change. Integrative and Comparative Biology 51: 719-732.

Krebs RA & Loeschcke V (1994) Costs and benefits of activation of the heat-shock response in *Drosophila melanogaster*. Functional Ecology 8: 730-737.

Kultz D (2005) Molecular and evolutionary basis of the cellular stress response. Annual Review of Physiology 67: 225-257.

Macqueen D, Robb D, Olsen T, Melstveit L, Paxton C & Johnston I (2008) Temperature until the 'eyed stage' of embryogenesis programmes the growth trajectory and muscle phenotype of adult Atlantic salmon. Biology Letters 4: 294-298.

Maia A de HN, Luiz AJB & Campanhola C (2000) Statistical inference on associated fertility life table parameters using Jackknife technique: computational aspects. Journal of Economic Entomology 93: 511-518.

Meehl GA & Tebaldi C (2004) More intense, more frequent, and longer lasting heat waves in the 21st century. Science 305: 994-997.

Metcalfe NB & Monaghan P (2001) Compensation for a bad start: grow now, pay later? Trends in Ecology and Evolution 16: 254-260.

Mironidis GK & Savopoulou-Soultani M (2010) Effects of heat shock on survival and reproduction of *Helicoverpa armigera* (Lepidoptera: Noctuidae) adults. Journal of Thermal Biology 35: 59-69.

Nafus DM & Schreiner IH (1991) Review of the biology and control of the Asian corn borer,

Ostrinia furnacalis (Lep: Pyralidae). International Journal of Pest Management 37: 41-56.

Nonci N (2004) Biology and natural enemies of Asian corn barer, *Ostrinia furnacalis* Guenée (Lepidoptera: Pyralidae) on corn. Jurnal Litbang Pertanian 23: 8-14.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution and Systematics 37: 637-669.

Pauli D, Arrigo AP & Tissieres A (1992) Heat shock response in *Drosophila*. Experientia 48: 623-629.

Perkins SE & Alexander LV (2013) On the measurement of heat waves. Journal of Climate 26: 4500-4517.

Potter KA, Davidowitz G & Woods HA (2011) Cross-stage consequences of egg temperature in the insect *Manduca sexta*. Functional Ecology 25: 548-556.

Potter K, Davidowitz G & Woods HA (2009) Insect eggs protected from high temperatures by limited homeothermy of plant leaves. Journal of Experimental Biology 212: 3448–3454.

Qayyum A & Zalucki MP (1987) Effects of high temperature on survival of eggs of *Heliothis armigera* (Hübner) and *H. punctigera* Wallengren (Lepidoptera: Noctuidae). Australian Journal of Entomology 26: 295-298.

Quan YD, He KL, Wang ZY & Wei HY (2015) Effects of transient exposure to extremely high temperatures on egg, neonate and adult of *Ostrinia furnacalis*. Plant Protection 42: 985-990. (In Chinese with English abstract)

Robinson PJ (2001) On the definition of a heat wave. Journal of Applied Meteorology 40: 762-775.

Sambucetti P, Scannapieco AC, Loeschcke V & Norry FM (2013) Heat-stress survival in the pre-adult stage of the life cycle in an intercontinental set of recombinant inbred lines of *Drosophila melanogaster*. Journal of Experimental Biology 216: 2953-2959.

Schreiner IH, Nafus DM & Dumaliang N (1990) Growth and survival of the Asian corn borer *Ostrinia furnacalis* Guenée (Lep: Pyralidae) on alternative hosts in Guam. Tropical Pest Management 36: 93-96.

Simpson SJ & Simpson CL (1990) The mechanisms of nutritional compensation by phytophagous insects. Insect-Plant Interactions, Volume 2 (ed. by EA Bernays), pp. 111-160. CRC Press, Boca Raton, FL, USA.

Southwood TRE (1977) Habitat, the templet for ecological strategies? Journal of Animal Ecology 46: 337-365.

Taylor BW, Anderson CR & Peckarsky BL (1998) Effects of size at metamorphosis on

stonefly fecundity, longevity, and reproductive success. Oecologia 114: 494-502.

Wang S, Michaud JP, Zhan RZ, Zhang F & Liu S (2009a) Seasonal cycles of assortative mating and reproductive behaviour in polymorphic populations of *Harmonia axyridis* in China. Ecological Entomology 34: 483-494.

Wang XG, Johnson MW, Daane KM & Nadel H (2009b) High summer temperatures affect the survival and reproduction of olive fruit fly (Diptera: Tephritidae). Environmental Entomology 38: 1496-1504.

Whitman D & Ananthakrishnan TN (2009) Phenotypic Plasticity of Insects: Mechanisms and Consequences. Science Publishers, Enfield, NH, USA.

Willmer P, Stone G & Johnston IA (2000) Environmental Physiology of Animals. Blackwell Publishing, New York, NY, USA.

Woods HA (1999) Patterns and mechanisms of growth of fifth-instar *Manduca sexta* caterpillars following exposure to low-or high-protein food during early instars. Physiological and Biochemical Zoology 72: 445-454.

Xia JJ, Tu K, Yan ZW & Qi YJ (2016) The super-heat wave in eastern China during July–August 2013: a perspective of climate change. International Journal of Climatology 36: 1291-1298.

Xie HC, Li DS, Zhang HG, Mason CE, Wang ZY et al. (2015) Seasonal and geographical variation in diapause and cold hardiness of the Asian corn borer, *Ostrinia furnacalis*. Insect Science 22: 578-586.

Xu JF, Deng ZY & Chen M (2009) A summary of studying on characteristics of high temperature and heat wave damage in China. Journal of Arid Meteorology 27: 163-167. (In Chinese with English abstract)

Xu B, Xu AH & Tang CS (2003) Severe high temperature analysis in Jiangxi during summer 2003. Jiangxi Meteorological Science and Technology 26: 27-29.

Yan ZW, Jones PD, Davies TD, Moberg A, Bergstrom H et al. (2002) Trends of extreme temperatures in Europe and China based on daily observations. Climatic Change 53: 355–392.

Yang Y & Joern A (1994) Compensatory feeding in response to variable food quality by *Melanoplus differentialis*. Physiological Entomology 19: 15-82.

Zhang Q, Xu CY, Zhang Z, Ren G & Chen YD (2008) Climate change or variability? The case of Yellow river as indicated by extreme maximum and minimum air temperature during 1960–2004. Theoretical and Applied Climatology 93: 35-43.

Zhang SY, Zhang HD, Xu XD, Zhang DK, Liao YM & Song YL (2005) Climatic character

and cause analysis of summer high temperature in main cities of east China. Plateau Meteorology 24: 829-835.

Zhou J, Liu Q, Han Y & Dong H (2018) High temperature tolerance and thermal-adaptability plasticity of Asian corn borer (*Ostrinia furnacalis* Guenée) after a single extreme heat wave at the egg stage. Journal of Asia-Pacific Entomology 21: 1040-1047.

Zhou DR & He KL (1995) The Integrated Control Technology of Corn Borer. Golden Shield Press, Beijing, China.

Figure captions

Figure 1 Mean (± SE) rates (%) of (A) egg hatching and (B) survival of *Ostrinia furnacalis* after heat shock treatment of the egg stage at various temperatures. Survival rate refers to insects that reached the adult stage to complete the life cycle. Means within a panel marked with different letters are significantly different (χ^2 test: $P<0.05$).

Figure 2 Mean (± SE) developmental time (days) for (A) larva, (B) pupa, and (C) adult stages, and (D) life span of *Ostrinia furnacalis* subsequent to various heat shock treatments of the egg stage. Means within a panel and within a sex marked with different letters are significantly different (LSD test: $P<0.05$).

Figure 3 Mean (± SE) (A) growth rate (% per day), (B) pupal mass (mg), (C) fecundity (no. eggs per female), (D) and female-to-male sex ratio of *Ostrinia furnacalis* following various heat shock treatments at the egg stage. Means within a sex marked with different letters are significantly different (growth rate: Kruskal-Wallis / Mann-Whitney test; other parameters: LSD test; all $P<0.05$).

Figure 4 Profiles of adult male and female emergence (%) as a function of egg to adult developmental period (days) of *Ostrinia furnacalis* following different heat shock treatments at the egg stage.

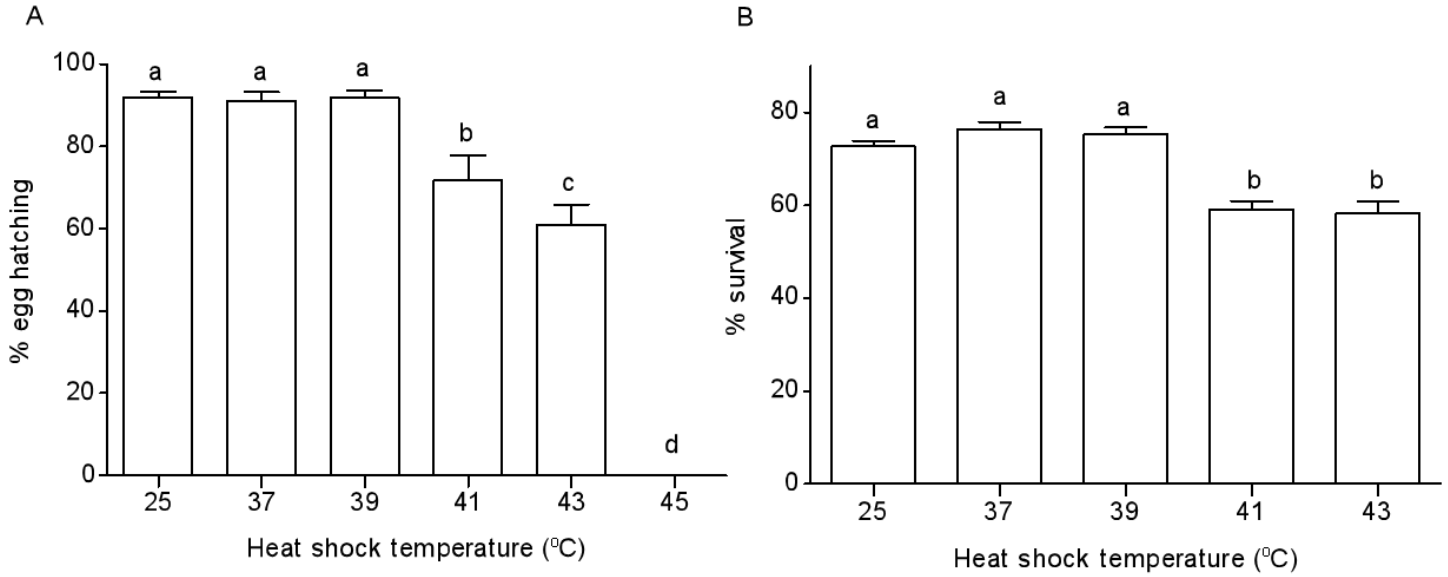
Accepted Manuscript
Version of record at: https://doi.org/10.1111/eea.13262

Table 1 Mean (± SE) life table parameters of *Ostrinia furnacalis* exposed to heat shock treatments at the egg stage (including females and males combined)

Heat shock temperature (°C)	Net reproductive rate (R_0)	Generation time (**t**) (days)	Innate capacity for increase (r_m)	Finite rates of increase (λ)
25	40.73 ± 2.95ab	28.19 ± 0.146a	0.1313 ± 0.0026ab	1.1403 ± 0.0030ab
37	47.94 ± 5.01a	28.12 ± 0.123a	0.1372 ± 0.0040a	1.1471 ± 0.0045a
39	43.86 ± 3.40ab	27.89 ± 0.121a	0.1354 ± 0.0027a	1.1450 ± 0.0031a
41	35.79 ± 1.61b	28.75 ± 0.130b	0.1244 ± 0.0015b	1.1324 ± 0.0017b
43	39.07 ± 1.64ab	29.29 ± 0.155c	0.1251 ± 0.0015b	1.1332 ± 0.0017b

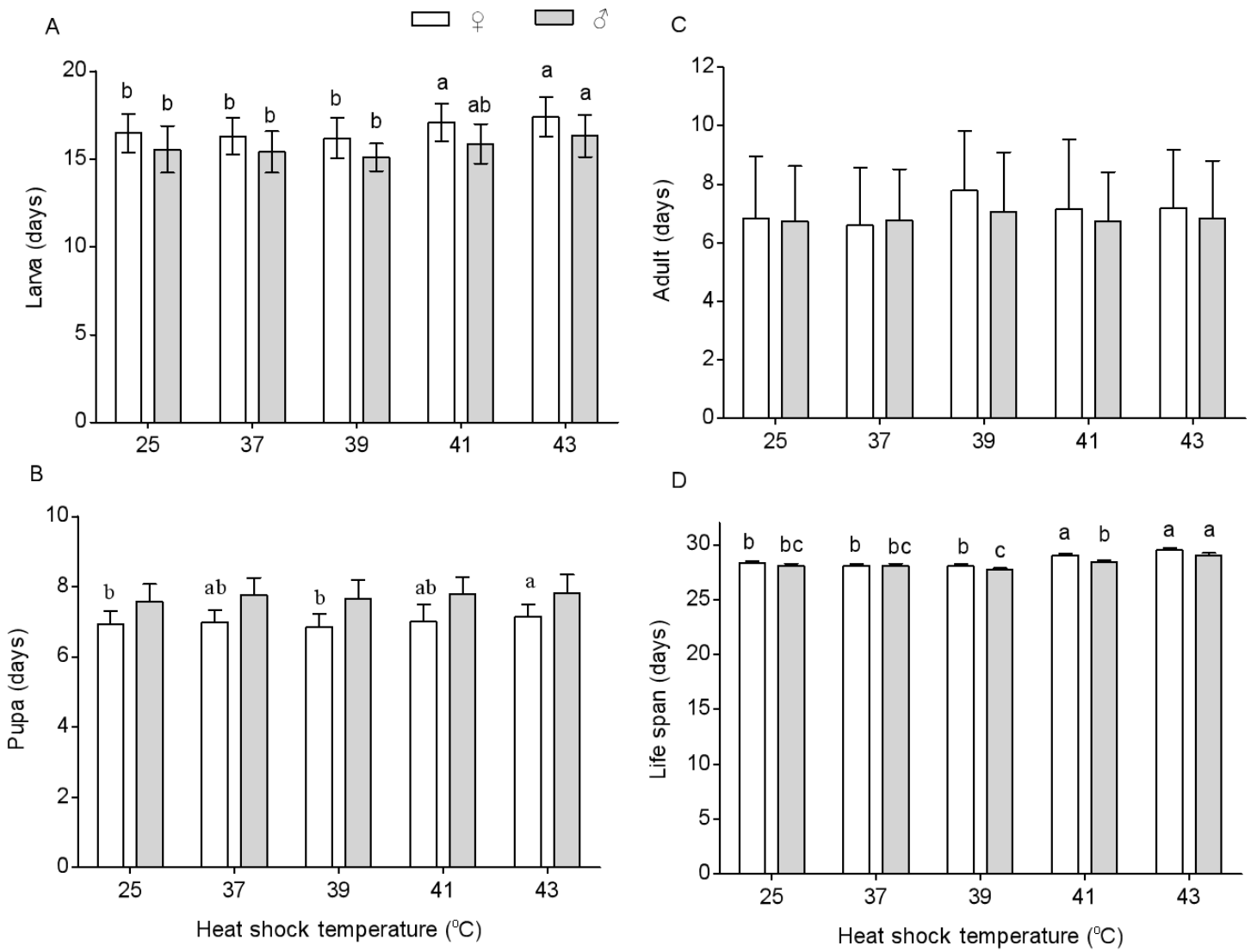
Means within a column followed by a different letter are significantly different (LSD test: $P<0.05$).

Accepted Manuscript
Version of record at: https://doi.org/10.1111/eea.13262



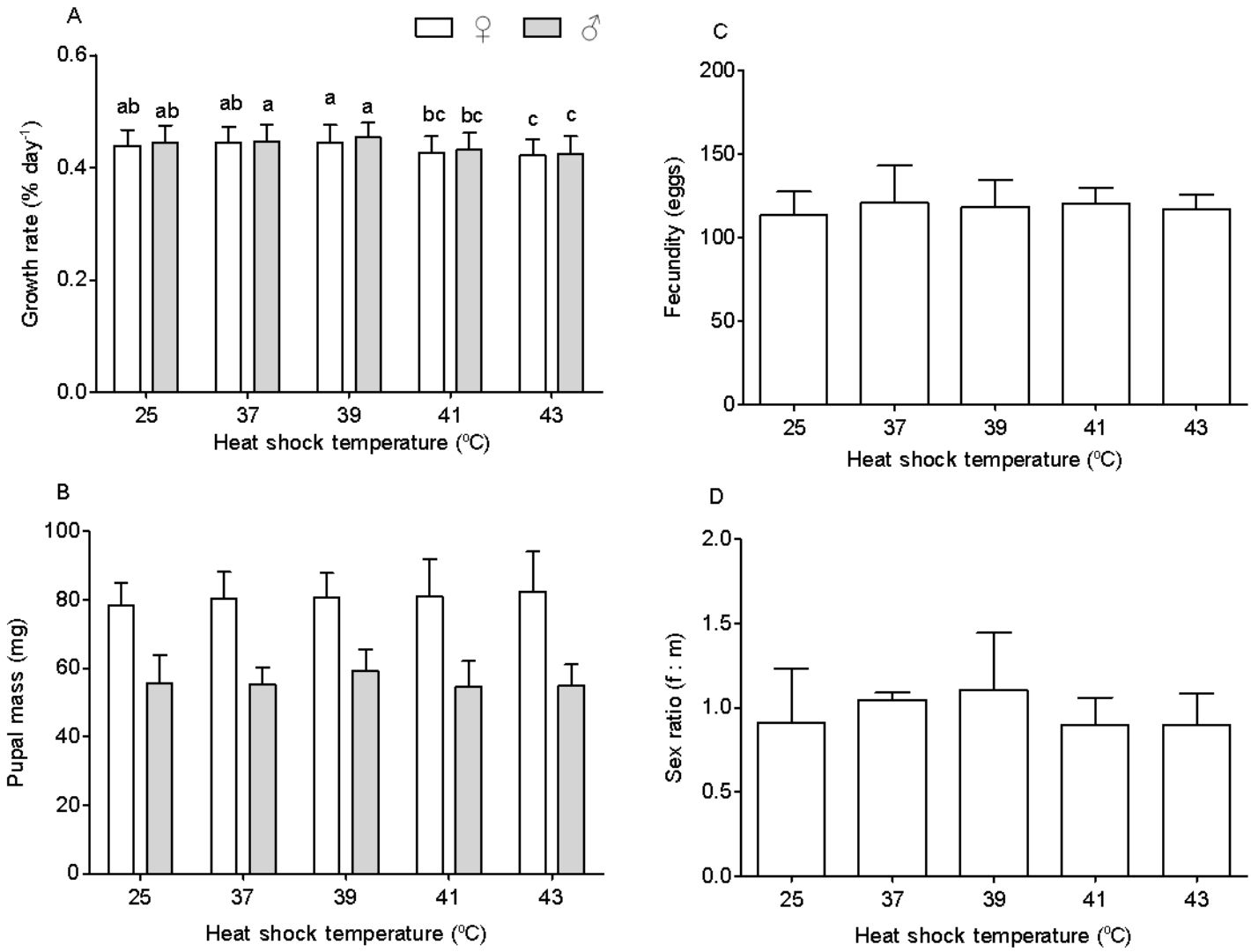
EEA_13262_Figure-1.tif

Accepted Manuscript
Version of record at: https://doi.org/10.1111/eea.13262



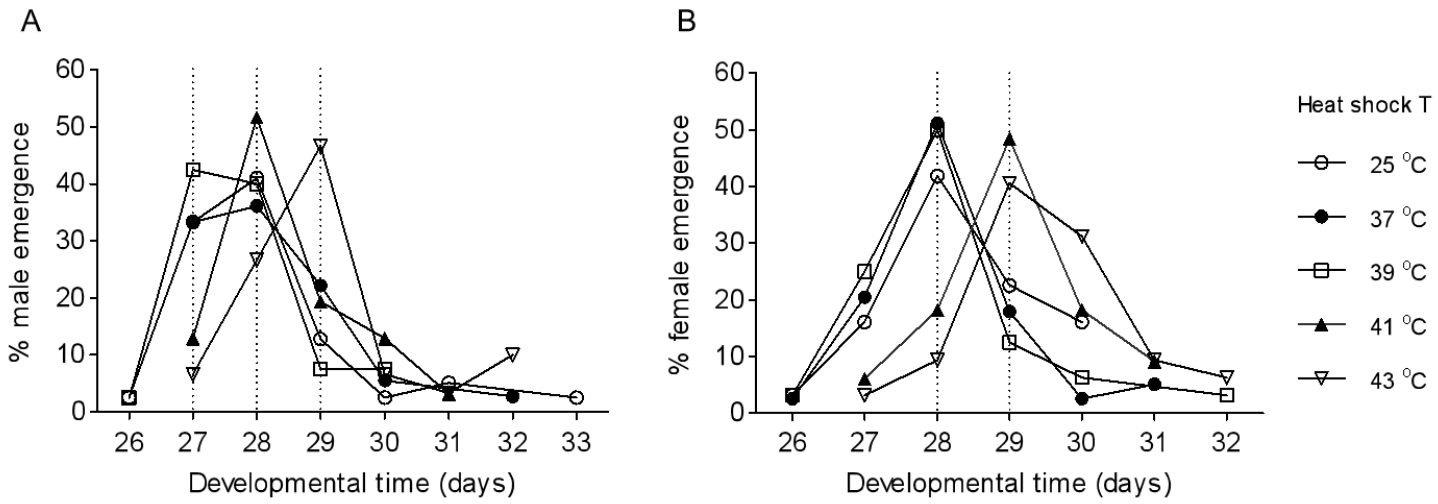
EEA_13262_Figure-2.tif

Accepted Manuscript
Version of record at: https://doi.org/10.1111/eea.13262



EEA_13262_Figure-3.tif

Accepted Manuscript
Version of record at: https://doi.org/10.1111/eea.13262



EEA_13262_Figure-4.tif