Journal of Thermal Biology 39 (2014) 40–44

Contents lists available at ScienceDirect

Journal of Thermal Biology

journal homepage: www.elsevier.com/locate/jtherbio

Exposing eggs to high temperatures affects the development, survival and reproduction of *Harmonia axyridis*

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ARTICLE INFO

Article history:
Received 28 April 2013
Accepted 17 November 2013
Available online 25 November 2013

Keywords:
Harmonia axyridis
Heat stress
Survival
Longevity
Reproduction

ABSTRACT

The multicolored Asian lady beetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), is a well-known biological control agent for aphids and soft-bodied insects. We investigated the developmental, survival and reproductive traits of *H. axyridis* when its eggs were exposed to 25 (control), 37, 39 and 41 °C for 1 h, and then transferred to ambient condition (25 °C). The effects of heat stress on the hatching success greatly differed among temperature treatments. No *H. axyridis* larvae hatched out at 41 °C. The development, survival, weight, reproduction and longevity of *H. axyridis* exhibited significant differences with temperature treatment and gender. The survival rate of immatures declined, while the adult fresh weight of both sexes markedly increased with the increase of temperature. Heat exposure of the eggs caused a subsequent reduction in longevity, oviposition period and reproduction, while the pre-oviposition period became longer as the temperature increased. These may imply that the reproductive investment increased in higher level stressful environments, and the response of adult individuals could be linked to the experiences from early stages of the life history. Our findings provide useful information for predicting population dynamics and understanding the potential for *H. axyridis* as a biological control agent under variable environments.

1. Introduction

Temperature is one of the most important ecological factors affecting growth, reproduction, distribution, abundance and phonology, and even small changes potentially have a significant impact on fitness and life history characteristics of insects (Angilletta et al., 2002; Bale et al., 2002; Parmesan, 2006; Wang et al., 2009b). The rate of global warming in the future is expected to increase much faster than that in the last century, and global mean surface temperature is predicted to increase by 1.5–6.0 °C by the end of this century (IPCC, 2007). There is no doubt that global warming will increase the exposure of insects and other ectothermic species to high temperatures exceeding their upper physiological limits (Deutsch et al., 2008). Temperatures above the normal optimum are perceived as heat stress by all living organisms. Heat stress may result in water loss (Yoder et al., 2009), disruption of structure of membranes (Hochachka and Somero, 2002), protein denaturation (Chown and Nicholson, 2004), and damage in neurons (Robertson, 2004; Chown and Terblanche, 2006). These injuries can lead to severe fitness consequences such as decreased growth and development and increased mortality (Krebs and Loeschcke, 1994; Hoffmann et al., 2003; Mironidis and Savopoulou-Soultani, 2010). When threatened by extreme temperatures, most insect species employ behavioral, physiological or genetic adaptation mechanisms to adjust their body temperature, or the extremes they can withstand (McMillan et al., 2005; Overgaard and Sorenson, 2008; Kalosaka et al., 2009; Nyamukondiwa and Terblanche, 2009; Karl et al., 2011). The eggs are the initial stage of insects' life cycles, and they have an upper and a lower temperature limits that they can tolerate. The temperatures outside of the limits would retard or completely inhibit the insect's development or kill the insects (Heming, 2003). When embryonic development of insect eggs is stressed by environmental factors, especially temperature, subsequent development and reproduction could be affected. However, how the thermal environment experienced in early ontogeny affects biological characteristics of both sexes and thermal tolerance capacities in later development stages is not well-studied (Bowler and Terblanche, 2008).

The predaceous coccinellids are important natural enemies of numerous small phytophagous insects and acarines, and are therefore considered as potentially good biological control agents (Obrycki and Kring, 1998). Aphidophagous coccinellids occur in most cropping systems and their impact on aphid populations is known to be important (Hodek and Honek, 1996; Obrycki et al.,

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http://dx.doi.org/10.1016/j.jtherbio.2013.11.007

2009). Predaceous coccinellids represent a third trophic level, which must cope with their own thermal stress. To our knowledge, however, little is known about the impact of heat stress on the life history traits of aphidophagous coccinellids.

Harmonia axyridis (Pallas) (Coleoptera: Coccinellidae) is indigenous to many regions of Asia, and is a generalist predator that feeds primarily on aphids and soft-bodied insects as well as pollen and nectar (Koch, 2003; Pervez and Omkar, 2006; Pell et al., 2008; Lundgren, 2009). *H. axyridis* has several characteristics that make it useful for biological control of aphids, such as high voracity, dispersal capacity, multivoltine pattern of seasonal development and low host specificity (Koch, 2003; Brown et al., 2011). It has been used successfully in greenhouses, orchards, gardens, and outdoor crops for aphid management (Obrycki et al., 2009). The aphid *Megoura japonica* (Matsumura), a severe pest on a variety of fabaceous plants in the genus *Vicia* and *Lathyrus*, such as broad bean (*Vicia faba* L.), garden pea (*Pisum sativum* L.), soy bean [*Glycine max* (L.) Merr.], as well as grass pea (*Lathyrus sativus* L.), is one of the major prey species of *H. axyridis*.

In northern China, temperature is normally above 35 °C during summer months, and the highest temperature during the day could well exceed 40 °C (Climate Databases, Chinese Academy of Forestry). An interesting question concerning the effects of the temperature extremes is whether they affect the development and reproduction of *H. axyridis*. The present paper describes laboratory experiments designed to study the effect of brief exposure of *H. axyridis* eggs to high temperatures in an attempt to discover how the subsequent developmental and reproductive activity of *H. axyridis* are affected.

2. Materials and methods

2.1. Insect species

H. axyridis colony was initiated from approximately thirty pairs of adults, collected from a garden pea (*P. sativum* L.) field and a nearby corn field in the Experimental Farm of the Northwest A&F University (34°17′37.01″ N, 108°01′03.34″ E). The lady beetles were reared in mesh covered cages ($40 \times 40 \times 40$ cm^3). Four potted broad bean seedlings with aphids were placed in each cage, and the seedlings were replaced with fresh ones with aphids when necessary. The lady beetles were reared at 23 ± 1 °C, $50 \pm 10\%$ RH and 16 L: 8D for at least 2 generations, and were then used in all experiments. *M. japonica* culture was initiated in the laboratory using aphids collected on garden pea in the same location as the lady beetles. The culture was developed on potted broad bean plants in mesh covered cages ($60 \times 60 \times 60$ cm^3).

2.2. Effects of heat shock on *H. axyridis* preimaginal development

Newly laid eggs (less than 12 h old) of *H. axyridis* were randomly divided among four groups: one group were placed in Petri dishes (12.0 cm in diameter and 2.0 cm in height) at a constant temperature of 25 °C (control), while other three groups were separately heat-shocked for 1 h in Petri dishes in a climate chamber at 37, 39 and 41 °C, and were then transferred to 25 °C under an ambient conditions at L16: D8 h and RH $60 \pm 10\%$ in the laboratory. A piece of filter paper was placed at the bottom of the Petri dish, and a few drops of water were added as needed to maintain sufficient humidity. For each treatment about 90–120 *H. axyridis* eggs (each bean leaf with one egg mass, total three to five egg masses) were used. The eggs were inspected every 12 h and numbers of hatched larvae were recorded. The first instar larvae were individually transferred from Petri dishes to an experimental arena using a soft camel-hair brush. The arena consisted of a 100 mL centrifugal tube, and each tube contained a broad bean shoot with its end inserted into a 5 mL Eppendorf tube filled with water. The tube was covered with a fine muslin cloth, secured with a rubber band. Newly hatched first instars were individually placed in close vicinity to the prey. At least thirty newly hatched larvae (i.e., each larva as one replicate) were randomly selected for each experimental group. The aphid along with host plant shoot was supplied during the entire larval life span. Aphids were replaced every 12 h to avoid microbial contamination, and the broad bean shoot was replaced with a fresh one when necessary. The development duration for each immature stage of the predators was recorded, and newly-emerged adults were sexed and weighed individually using an electronic balance (Mettler-Toledo XS64, Switzerland) with a precision of 0.1 mg to record their initial body mass.

2.3. Effects of egg heat shock on longevity and reproduction of *H. axyridis* adults

To evaluate longevity and reproductive performance of the adults, individual newly-emerged adults from stressed eggs were sexed and paired. Each pair in each temperature treatment was placed in a transparent hard plastic truncated cylindrical cup (500 mL) covered with a fine muslin cloth. Along with the aphids, each cup contained a broad bean shoot with its end inserted into a 50 mL conical flask filled with water. The pair was transferred to a new cup twice a day until the female died, and the number of eggs laid each day was counted. Twenty pairs (i.e., each pair as one replicate) were selected for each experimental group. Pre-oviposition period, oviposition period, fecundity, and longevity were simultaneously determined. Females that did not lay any eggs were excluded from the analysis. The adults maintained at 25 °C under a L16: D8 h and RH $60 \pm 10\%$ were used as controls.

2.4. Statistical analysis

The effects of temperature on developmental time of immature stages were subjected to one-way analysis of variance (ANOVA). The effects of temperature and sex on developmental duration and adult weight were subjected to two-way ANOVA. The hatching rate and survival rate were arcsine-transformed and then analyzed using χ^2-test. All data were analyzed using the statistical package software SPSS 11.5 (2002).

3. Results

3.1. Development and survival of immature *H. axyridis*

The effects of heat shock on the eggs hatching greatly differed among temperature treatments. No *H. axyridis* larvae were hatched at 41 °C, so the hatching rates were compared with those eggs from 39, 37 or 25 °C. The eggs hatching rates were highest at 25 °C (92.6%), following at 37 °C (47.1%) and 39 °C (43.3%) (χ^2=24.407, df=2, $P<0.001$). The subsequently preimaginal developmental duration of *H. axyridis* exhibited significant differences with temperature treatment and sex (Table 1). The mean developmental durations of the first instars (F=0.472; df=2, 39; P=0.627), the second instars (F=2.070; df=2, 39; P=0.141), the third instars (F=1.816; df=2, 39; P=0.177), the pupae (F=1.095; df=2, 39; P=0.345), and the preimaginal development (F=1.276; df=2, 39; P=0.291) were not significantly different among the female larvae at different temperature treatments. However, the fourth instars (F=4.261; df=2, 39; P=0.022) showed significant difference. Similarly, the development durations of the first instars (F=1.314; df=2, 38; P=0.281), the second instars (F=1.570; df=2,