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Effect of parasitoid density on the timing of parasitism and development duration of progeny in *Sclerodermus pupariae* (Hymenoptera: Bethylidae)

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HIGHLIGHTS

- *Sclerodermus pupariae* parasitoid density affected adult and offspring performance.
- Intraspecific cooperation improved the parasitic efficacy of wasps on one host.
- The parasitoids well displayed mutually beneficial behaviors.

GRAPHICAL ABSTRACT

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ABSTRACT

The gregarious idiobiont ectoparasitoid, *Sclerodermus pupariae* Yang et Yao, is a natural enemy that parasitizes buprestid and cerambycid beetle larvae in China. In a recent laboratory study of mass–reared female parasitoids on larvae of the substitute host, *Thyestilla gebleri*, the subsequent offspring were widely released to control target pests. To develop cost–effective techniques for rearing parasitoids, and improve the parasitic efficiency of *Sclerodermus pupariae*, several parasitoid–host ratios have been investigated. However, the mechanism whereby increasing the density of inoculated female wasps on a host affects female parasitoid fitness (adult performance and progeny developmental duration) remains unclear. In the present study, we examined the influence of parasitoid density (one to eight female wasps per host) on the time to first attack, paralyzing time, pre–oviposition period and oviposition period of foundresses and developmental duration of offspring. We showed that the time to first attack, paralyzing time, pre–oviposition period and oviposition period of foundresses were significantly negatively associated with parasitoid density, but that developmental duration of progeny was only affected at the larval stage. An increase in the parasitoid density to more than three female wasps per host had no significant influence on the investigated parameters. Our results suggest that host nutrition was adequate, and intraspecific interaction enhanced the parasitic efficiency of wasps sharing a single host. Furthermore, it is known that a suitable parasitoid–host ratio can play an important role in promoting mutually beneficial behaviors which enhance adult performance.

1. Introduction

Parasitoid wasps of the family Bethylidae are widely used as biological control agents for some woodborer beetles in Asia (Tang et al., 2012; Wang, 2005; Wang et al., 2010; Yang et al.,

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2013). For example, *Scleroderma guani* is one of the most widely used natural enemy species of small and medium sized larvae of several long–horned beetles in China (Chen and Cheng, 2000; Huang et al., 2006; Ma, 2007; Xiao and Wu, 1983; Xu et al., 2002; Yao and Yang, 2008; Zhou and Yang, 1997). The gregarious idiobiont ectoparasitoid *Sclerodermus pupariae* Yang et Yao (Hymenoptera: Bethylidae) is a species newly discovered from Tianjin, China. This species which parasitizes the pupal or late larval stages of the emerald ash borer beetle, *Agrilus planipennis*, has been found in northern China, 15 states of the USA, and two provinces of Canada, where it causes substantial economic and environmental damage (Yang et al., 2012; Haack et al., 2002).

Sclerodermus pupariae overwinters as apterous females in emerald ash borer galleries or in ash bark crevices and emerges in late June. When a female parasitoid locates an *A. planipennis* larva, the duration of the pre–oviposition period is approximately one week; the female then lays 26–58 eggs, depending on host size. Eggs hatch within approximately 2 d, and the larvae develop within one week at 25 °C. The duration of the pupal stage last is 15–20 d and 24–56 adult wasps are produced per brood. The average sex ratio is 22:1 females to males. During the developmental period of offspring, the female parasitoids provide maternal care. This consists of the following aspects: (i) the female cleans the host body removing frass and dirt; (ii) if any eggs or larvae fall off the host, the female picks them up and replace them on the host; (iii) if any of the progeny are infested by bacteria or fungi, the female moves these larvae far from the brood and excretes an antibiotic substance to prevent microbial spread; (iv) the mothers leave their progeny to search for additional hosts only after the offspring have successfully emerged as adults (Wu et al., 2008a; Yang et al., 2012).

Under laboratory or field conditions, *Sclerodermus pupariae* also attacks major pests of trees such as wild apple trees, pine wood, deciduous broadleaf tree species, oak trees and other landscaping greening trees specie in China (Tang et al., 2014b; Wu et al., 2008b; Wang et al., 2010, 2014). Previous studies have mainly focused on the mechanism whereby this generalist parasitoid adapts to different–sized hosts under a one wasp–one host relationship. Wei et al. (2014) found that *S. pupariae* optimized its developmental times and progeny size according to the abundance of different–sized beetle larvae (*Massicus raddei*). Furthermore, the parasitic efficiency on novel hosts was enhanced by learning experience (Wei et al., 2013). These findings indicate that *S. pupariae* is an important natural enemy and population controller of wood borer beetles in China, and that this parasitoid has strong host searching and attacking abilities.

The success of biological control with inundative parasitoid releases depends, in part, on the efficiency and quality of the artificial mass–rearing system (Chambers, 1977). Currently, the larvae of *Saperda populnea* and the pupae of *Tenebrio molitor* have been used as substitute hosts for artificially mass–rearing *S. guani*. Additionally, our laboratory has reported that the long–horned beetle larva, *Thyestilla gebleri*, is high–quality substitute host of *Sclerodermus* due to its comparatively large body size. Furthermore, the self–defense behaviors of *T. gebleri* are typically very weak. In general, a middle–instar *T. gebleri* larva can be successfully parasitized by a single *S. pupariae* female. However, artificially mass–rearing *S. pupariae* has led to several problems as follows: (i) a single wasp can paralyze a large host because of its strong aggressive behaviors; (ii) the offspring of a single maternal wasp cannot effectively utilize all host resources; and (iii) if the parasitoid density is increased, two or more wasps can share a single host (quasi–sociality, Tang et al., 2014a), and this directly induces higher a parasitism rate and enhanced host utilization.

The objective of our present study was to examine the effect of the number of female founders on the timing of parasitism and on the developmental duration of progeny. We compared parasitism parameters such as time to first attack, time to paralysis, pre–oviposition period, oviposition period and development durations of offspring at various maternal parasitoid densities.

2. Materials and methods

2.1. Experimental materials

We established our laboratory population of *S. pupariae* from *A. planipennis* larvae collected in the late autumn of 2011 at Guangang Forest Park, Dagang District, Tianjin, China. Prior to our experiment, we reared 30 generations of parasitoids on *T. gebleri* larvae in the laboratory to exclude the possible influences of the host source (King, 1987). The parasitoids were maintained at 25 ± 5 °C and 60–70% RH under a LD 10:14 h light regime. The substitute host species (*T. gebleri*) used in mass–rearing *S. pupariae*, was collected from Tianjin, China. Host larvae were weighed using an analytical balance (sensitivity 0.1 mg), and 96 larvae (weight range 200.0–240.0 mg) were selected for our experiment. Although there was a 40 mg variation among the hosts used, our preliminary test indicated that the interaction between host weight and foundress numbers were not significant. We regarded host size as a constant.

2.2. Inoculation of Sclerodermus pupariae

We randomly selected 432 mated and healthy female wasps with an average age of one week after emergence. Individual hosts were exposed to different numbers of female parasitoids (from one to eight) in a vial (5 × 1 cm). The opening of each vial was blocked with a cotton plug. We conducted 12 trials for each of the eight parasitoid–host ratios examined. All experimental insects were maintained in an artificial–climate chamber at 25 ± 1 °C and RH 60–70%, under a LD 14:10 h light regime.

2.3. Observation of female parasitoid performance

We defined the time to first attack as the period between inoculation and the first wasp sting (to the host). Furthermore, the period between the first wasp sting and the onset of paralysis in host larvae was defined as the paralysis time. We monitored the time to first attack and paralysis time every 20 min. *S. pupariae* is a synovigenic parasitoid, with oogenesis occurring after females are stimulated by feeding on host hemolymph (Wei et al., 2014). Hence, we defined the pre–oviposition period as the time interval between host paralysis and the first egg laid. We defined the oviposition period as the period between the first and last eggs laid.

2.4. Parasitoid offspring developmental processes at different maternal densities

We monitored the developmental processes of parasitoid offspring (oviposition to emergence) for each replicate. The egg stage was calculated as the time interval between the first egg laid and the first larva emergence. We defined the larval stage as the period between the emergence of the first larva and the first cocoon. Finally, the pupal stage was considered the time interval between the emergence of the first cocoon and the first adult. All parasitized hosts were observed twice daily under a microscope.

2.5. Data analysis and statistics

All observations were recorded using Windows Excel 2003. We used one–way analysis of variance (ANOVA) to assess the differences among means in adult performance (time to first attack,