Effects of Host Ages and Release Strategies on the Performance of the Pupal Parasitoid Spalangia endius on the Melon Fly Bactrocera cucurbitae

Jian-Feng Liu 1,2, Cheng-Xu Wu 3, Atif Idrees 3, Hai-Yan Zhao 4,* and Mao-Fa Yang 2,4,*

1 State Key Laboratory Breeding Base of Green Pesticide and Agricultural Bioengineering, Key Laboratory of Green Pesticide and Agricultural Bioengineering, Ministry of Education, Guizhou University, Guiyang 550025, China
2 Institute of Entomology, Guizhou University, Guizhou Provincial Key Laboratory for Agricultural Pest Management of the Mountainous Region, Scientific Observing and Experimental Station of Crop Pest in Guizhou, Ministry of Agriculture, Guizhou 550025, China
3 College of Forestry, Guizhou University, Guiyang 550025, China
4 College of Tobacco Science, Guizhou University, Guiyang 550025, China
* Correspondence: hyzhao@gzu.edu.cn (H.-Y.Z.); mfyang@gzu.edu.cn (M.-F.Y.)

Abstract: The melon fly, Bactrocera cucurbitae Coquillett (Diptera: Tephritidae), is a quarantine pest that causes considerable economic losses to growers of vegetables and fruits worldwide. Spalangia endius (Walker) (Hymenoptera: Pteromalidae) is a solitary pupal parasitoid of various dipteran hosts. We assessed the impact of the host pupal age (2, 4, and 6 days old), host density (5, 10, 15, 20, 25, and 30), and parasitoid density (1, 2, 3, 4, 5, and 6) on the parasitizing potential of S. endius on B. cucurbitae pupae under laboratory conditions. The effects of different soil depths on the parasitism rate of S. endius and the dispersal behavior of S. endius at distances of 0, 5, and 10 m were also evaluated under field conditions. The results showed that the parasitism rate of S. endius significantly increased with the increase in host density and parasitoid density. The host pupal age did not influence the number of pupae parasitized by S. endius and the progeny sex ratio of S. endius under different host densities. In the fields, different puparium burial depths of B. dorsalis pupae significantly influenced the parasitism and eclosion rates of S. endius but did not influence the eclosion rate of B. cucurbitae. Spalangia endius females could travel up to 10 m to parasitize at a similar rate on B. cucurbitae pupae compared to S. endius placed at 0 m.

Keywords: biological control; melon fly; parasitoid; depth; dispersal; Spalangia endius; Bactrocera cucurbitae

1. Introduction

The melon fly, Bactrocera cucurbitae Coquillett (Diptera: Tephritidae), is a worldwide quarantine pest and causes considerable economic losses and substantial damages to the growers of vegetables and fruits in temperate, tropical, and sub-tropical regions [1] and to various agricultural products, including watermelon, cucumber, and courgette [2,3]. Bactrocera cucurbitae has also severely impeded international trade due to strict quarantine regulations.

Control measures frequently focus on the extensive use of chemical insecticides, bait traps, and sterile insect techniques (SITs) aiming at mature fruit fly adults [4,5]. However, chemical insecticides are harmful to humans and the environment and beneficial to non-target fauna. SITs, although they have some success in managing B. cucurbitae in isolated regions [6], are unsuitable in continental areas because of the fly’s long-distance migratory ability, long pre-copulatory period, and polyandrous nature [7]. Bait traps have limited success because they lure only males. Identifying effective control measures for B.
cucurbitae that are safe for humans, non-target organisms, and the environment is essential. Biological control strategies are likely to play a crucial role in this process. There has been an increasing interest in selecting more effective parasitoids as the biological control agents of B. cucurbitae. The idiobiont ectoparasitoid Spalangia endius (Walker) (Hymenoptera: Pteromalidae) hosts numerous dipteran species belonging to Tephritidae, Sarcophagidae, Muscidae, Calliphoridae, and Anthomyiidae [8]. This parasitoid is a solitary pupal parasitoid and has been commercialized for the biological control of dipterans, including several Drosophila species [9,10], Musca domestica and Stomoxys calcitrans [11–13], and B. cucurbitae, B. dorsalis [14], and Ceratitis capitata (Wiedemann) [15].

In biological control programs, one of the criteria for predicting parasitoids’ success as control agents is related to the behavior of individual predators, such as parasitoids, in response to the changes in prey density [16,17]. The foraging efficiency of pupal parasitoids is associated with the pupation depth of hosts in soil [18]. The majority of Bactrocera (Dacus) oleae (Gmel.) larvae pupate in the top 3 cm of soil with a mean depth of 1.16 cm, which is influenced by the types, temperatures, and levels of compaction and moisture of soil [19]. Geden (2002) showed that five species of pupal parasitoids could not attack the house fly pupae that were buried in sandy loam soil at any depth but could search over a wider range of depths in the fly larval rearing medium [20]. The pupal parasitoid, Nasonia vitripennis Walker, only parasitizes the pupae of Calliphora vicina Robineau-Desvoidy at 0 cm depth [21]. However, there is little information on the effect of the puparium burial depths of hosts on the parasitic ability of S. endius.

The dispersal ability of parasitoids is another major determinant for understanding the movement of individual parasitoid females [22]. A large number of parasitoids must be released over a long period to effectively control pests [23]. An 8-month release of Dichasimimorpha longicaudata (Ashmead) at 20,000–60,000/km²/week within a 13 km² area in Florida reduced the Anastrepha suspensa (Loew) population by 95% [24]. A negative relationship was found between the parasitism level and parasitoids’ releasing distance [25].

Previous studies evaluated the effect of host pupal age of Bactrocera dorsalis Hendel on the preference and host suitability of the pupal parasitoid S. endius [26]. Spalangia cameroni Perkins caused the highest rate of total parasitism on Musca domestica Linnaeus within 5 m of the release site [27]. However, relatively little is known about the effect of the suitability and density of B. cucurbitae pupae and release strategies on the performance of S. endius. Here, this study aimed to evaluate the impact of host pupal age (2, 4, and 6 days old), host density (5, 10, 15, 20, 25, and 30), and parasitoid density (1, 2, 3, 4, 5, and 6) on the parasitizing potential of S. endius on B. cucurbitae pupae under laboratory conditions. The effects of different soil depths of B. cucurbitae on the parasitism rate of S. endius and its dispersal behavior were also evaluated under field conditions.

2. Materials and Methods
2.1. Insect Cultures

Bactrocera cucurbitae individuals were mass-reared on a banana-based artificial diet (50 g cornflour, 150 g banana, 0.6 g sodium benzoate, 30 g yeast, 30 g sucrose, 30 g winding paper, 1.2 mL hydrochloric acid, and 300 mL water) in the laboratory at the Hainan Academy of Agricultural Sciences, Hainan Key Laboratory for Control of Plant Diseases and Insect Pests, Haikou, China. Adults were fed a 1:1 sucrose:yeast diet. Three-day-old host pupae were used for experiments.

Spalangia endius individuals were originally obtained from the pupae of field-collected B. cucurbitae in orchards. The parasitoids were reared continuously on B. cucurbitae pupae in our laboratory for more than 25 generations. Newly emerged adult parasitoids were kept in insect-rearing cages (25 × 25 × 30 cm) at a density of 50–100 pairs and provided with 15% honey water daily. After parasitoid emergence, female and male parasitoids were kept in the same cage with food but without hosts. Two-day-old mated female parasitoids were used for experiments.
The cultures and experiments were conducted in a climate-controlled room at a temperature of 25 ± 1°C, relative humidity of 70 ± 2%, and a 14:10 (light:dark) photoperiod.

2.2. Parasitization at Constant Parasitoid Density and Variable Host Density

The 2-, 4-, and 6-day-old *B. cucurbitae* pupae were placed separately at densities of 5, 10, 15, 20, 25, and 30 pupae in 1000 mL glass tubes. A single female *S. endius* (aged: 2 days) was released into each glass tube for oviposition for 24 h. The parasitoid was then removed from the tube. The host pupae were transferred into 100 mL plastic cups and covered with humid sand. The opening of the plastic cup was covered with a fine nylon mesh (120 meshes). The pupae were kept in the cups until the emergence of the parasitoids. The emerged parasitoids were then kept in a room at a temperature of 25–27°C. Thirty replicates were prepared for each pupal stage with a single parasitoid. After the parasitoids and flies emerged completely, the number of parasitized fruit fly pupae was counted and recorded.

2.3. Parasitization at Constant Host Density and Variable Parasitoid Density

Female parasitoids (aged: 2 days) were placed in a 1 L beaker at the densities of 1, 2, 3, 4, 5, and 6 parasitoids, separately, with 50 *B. cucurbitae* pupae (3 days old) in each beaker. The parasitoids were removed from each beaker after 24 h, and the host pupae were transferred to 100 mL plastic cups and covered with humid sand until the emergence of the parasitoids at 25–27°C. The opening of the plastic cup was covered with a fine nylon mesh (120 meshes). In total, 30 replicates were used for each parasitoid density with 50 *B. cucurbitae* pupae. After all the parasitoids and flies emerged, the number of parasitized fruit fly pupae was counted and recorded.

2.4. Releasing Techniques of *S. endius* against *B. cucurbitae* in Field

**Different host depths in soil:** To evaluate the effect of the soil depths of hosts on the performance of *S. endius*, we buried *B. cucurbitae* pupae at 6 soil depths (0, 1, 2, 3, 4, and 5 cm from soil surface) with sandy loam soil in a 120-mesh cage (1.5 m length × 1 m width × 2.0 m height). We released 10 mated *S. endius* females into the cage. Each soil depth was replicated 10 times, and each replication had 20 *B. cucurbitae* pupae (aged: 3 days). After 7 days, we dug out the pupae of *B. cucurbitae* and determined the eclosion rate of *S. endius* and *B. cucurbitae*. Then, the non-eclosion pupae were dissected to observe whether they were parasitic, and the parasitism rate of *S. endius* was determined and recorded.

**Dispersal behavior of *S. endius***: In order to analyze the dispersal behavior of *S. endius*, thirty 3-day-old *B. cucurbitae* pupae were placed on the ground at distances of 0, 5, and 10 m from the central releasing point of *S. endius*. Ten mated *S. endius* females were either directly placed at the ground (0 m) or suspended up 1 and 2 m from the ground as the releasing point. After 24 h, the *B. cucurbitae* pupae were collected back to evaluate the eclosion rate of *S. endius*, and the non-eclosion pupae were dissected to observe whether they were parasitized, and the parasitism rate was determined. Ten replications were used for each treatment.

2.5. Data Analysis

Mortality (%) (*M* corrected) was calculated using the following formula:

\[
\text{Mortality} \% = \frac{[\text{M}_{\text{treatment}} - \text{Parasitism} \% - \text{M}_{\text{control}}]}{(100 - \text{M}_{\text{control}})} \times 100
\]  

Differences in the number of parasitized fruit flies, mortality, survival, and emergence rates as percentages were arcsine-transformed before being subject to statistical analysis. The transformed data were analyzed with one-way analysis of variance (ANOVA) followed by Tukey’s honestly significant difference (HSD) test (*p* < 0.05) using SPSS 16.0 software.
3. Results

3.1. Effects at a Constant Parasitoid Density and Varying Host Density

The mean number of *B. cucurbitae* pupae parasitized by *S. endius* females increased significantly with the increase in host pupa densities from 1.80% to 9.95%, 1.85% to 10.65%, and 1.75% to 9.45% on 2-, 4-, and 6- days old hosts, respectively (Table 1). However, the host age was not a major factor influencing the number of pupae parasitized, except at 20 and 25 host densities (Table 1).

The average parasitoid sex ratios of *S. endius* parasitized old *B. cucurbitae* (0.685, 0.697, 0.651, and 0.658 ) for 4 days were slightly higher than those of the parasitoids parasitized for 2 days (0.665, 0.652, 0.603, and 0.610) and for 6 days (0.630, 0.685, 0.595, and 0.621) under the host densities of 10, 15, 25, and 30 pupae (Table 1), indicating that host age did not affect the progeny sex ratio. Moreover, host density had no influence on the proportion of males and females in the parasitoid progeny. When *S. endius* parasitized on 15 *B. cucurbitae* pupae, there were slightly higher sex ratios (0.652, 0.697, and 0.685) for 2-, 4-, and 6 days old hosts, respectively, compared to other host densities.

Table 1. Number of parasitized pupae and progeny sex ratio in *Spalangia endius* parasitizing *Bactrocera cucurbitae* pupae.

| Number of Pupae | Number of Parasitized Pupae | Parasitoid Sex Ratio |
|-----------------|-----------------------------|---------------------|
|                 | 2 Days Old | 4 Days Old | 6 Days Old | 2 Days Old | 4 Days Old | 6 Days Old |
| 5               | 1.80 ± 0.16 Ad | 1.85 ± 0.16 Ae | 1.75 ± 0.14 Ae | 0.575 ± 0.081 Aa | 0.558 ± 0.081 Aa | 0.550 ± 0.081 Aa |
| 10              | 3.80 ± 0.27 Ac | 4.05 ± 0.29 Ad | 3.65 ± 0.28 Ad | 0.665 ± 0.027 Aa | 0.685 ± 0.088 Aa | 0.630 ± 0.053 Aa |
| 15              | 5.95 ± 0.29 Ab | 6.05 ± 0.43 Ac | 5.60 ± 0.41 Ac | 0.652 ± 0.024 Aa | 0.697 ± 0.064 Aa | 0.685 ± 0.028 Aa |
| 20              | 8.40 ± 0.37 Ba | 8.85 ± 0.60 Ab | 7.80 ± 0.47 Bbc | 0.624 ± 0.019 Aa | 0.639 ± 0.044 Aa | 0.663 ± 0.052 Aa |
| 25              | 9.25 ± 0.45 Ba | 9.90 ± 0.52 Aab | 8.80 ± 0.45 Bab | 0.603 ± 0.036 Aa | 0.651 ± 0.042 Aa | 0.595 ± 0.043 Aa |
| 30              | 9.95 ± 0.47 Aa | 10.65 ± 0.60 Ab | 9.45 ± 0.60 Aa | 0.610 ± 0.026 Aa | 0.658 ± 0.042 Aa | 0.621 ± 0.025 Aa |

Means followed by the same lowercase letter (columns) or capital letter (row) are not significantly different according to Tukey’s HSD multiple range test ($p > 0.05$).

3.2. Effect of Parasitoid Density

The total percentage of parasitism increased as the parasitoid density increased from one to six individuals, but the number of *B. cucurbitae* parasitized by each individual *S. endius* decreased significantly with the increase in the parasitoid density (Table 2). Thus, increasing parasitoid density adversely affected the performance of individual parasitoids. Releasing one and six *S. endius* achieved the lowest and highest total parasitism on *B. cucurbitae*, respectively. At the same time, there was no significant difference in the number of *B. cucurbitae* parasitized by three, four, and five *S. endius* (Table 2).

The parasitoid progeny was always female-biased, but the female proportion of *B. cucurbitae* decreased from 65.52% to 61.53% as the parasitoid density increased (Table 2). The emergence rates of *S. endius* decreased slightly from 95.40% to 92.60% with the increase in the parasitoid density from one to six individuals, but no significant differences were observed in parasitoid emergence rates in relation to the parasitoid densities. Host mortality increased gradually with the increase in parasitoid density, reaching peak mortality (14.17%) at six individuals compared with minimum mortality (7.95%) at one individual.
Table 2. Effects of Spalangia endius parasitoid density in relation to the host pupae of Bactrocera cucurbitae.

| Parasitoid Number | Number of Pupae | Total Parasitism (%) | Parasitism per Female (%) | Emergence (%) | Sex Ratio (Female %) | Corrected Mortality (%) |
|-------------------|-----------------|-----------------------|---------------------------|--------------|----------------------|------------------------|
| 1                 | 50              | 20.48 ± 1.47 d        | 20.48 ± 1.47 a           | 95.40 ± 0.93 a | 65.52                | 7.95 ± 0.42 c          |
| 2                 | 50              | 35.04 ± 3.52 c        | 17.52 ± 1.76 ab          | 95.20 ± 0.97 a | 65.21                | 9.19 ± 0.92 bc         |
| 3                 | 50              | 47.12 ± 2.72 b        | 15.71 ± 0.91 c           | 94.40 ± 0.87 a | 64.24                | 10.38 ± 0.79 bc        |
| 4                 | 50              | 51.04 ± 2.43 b        | 12.76 ± 0.61 cd          | 94.00 ± 0.32 a | 63.55                | 11.26 ± 0.77 ab        |
| 5                 | 50              | 54.32 ± 2.44 ab       | 10.86 ± 0.49 d           | 93.60 ± 0.51 a | 62.24                | 12.96 ± 1.29 a         |
| 6                 | 50              | 61.20 ± 2.91 a        | 10.20 ± 0.48 d           | 92.60 ± 0.63 a | 61.53                | 14.17 ± 1.07 a         |

Means followed by the different lowercase letters (columns) are significantly different according to Tukey’s HSD multiple range test (p < 0.05).

3.3. Releasing Strategies of S. endius against B. cucurbitae

The parasitism of S. endius was significantly influenced by the depths of B. cucurbitae pupae in soil (Figure 1). No significant difference was observed in the parasitism rate of S. endius when the B. cucurbitae pupae were placed between 0 and 1 cm in the soil. The parasitism rate decreased significantly when the depth of the B. cucurbitae pupae in soil was increased from 2 cm to 5 cm. Spalangia endius could not parasitize the B. cucurbitae pupae at depths of 4 and 5 cm in the soil. In addition, the soil depths of the B. cucurbitae pupae did not affect the eclosion rate of S. endius. The depths (0, 2, 3, and 4 cm) of B. cucurbitae pupae in soil did not influence the eclosion rate of B. cucurbitae (Figure 1).

Spalangia endius female could travel up to 10 m to parasite B. cucurbitae pupae in soil with parasitism rates of 29.33%, 30.00%, and 28.67%, similar to 32.00%, 31.33%, and 29.33% of the pupae placed at 0 m at three different releasing heights. Different releasing heights did not affect the parasitism rate of S. endius on B. cucurbitae pupae under different diffusion distances (Table 3).

Figure 1. Effects of different soil depths on the parasitism and eclosion rates of Spalangia endius against Bactrocera cucurbitae and the eclosion rate of the host pupae. Means followed by the different
lowercase (columns) in each bar are significantly different according to Tukey’s HSD multiple range test \((p < 0.05)\).

Table 3. Dispersal behavior of *Spalangia endius* on *Bactrocera cucurbitae* pupae.

| Dispersal Range from Releasing | Different Releasing Heights |
|-------------------------------|-----------------------------|
|                               | 0 m | 1 m | 2 m |
| 0 m                           | 32.00 ± 1.69 aA | 31.33 ± 1.69 aA | 29.33 ± 1.94 aA |
| 5 m                           | 31.33 ± 1.33 aA | 30.67 ± 1.25 aA | 31.33 ± 1.33 aA |
| 10 m                          | 29.33 ± 1.24 aA | 30.00 ± 1.49 aA | 28.67 ± 1.70 aA |

The same lowercase or capital letters indicate no significant differences in the parasitism rate of *S. endius* on *B. cucurbitae* pupae among different diffusion distances or different releasing heights according to Tukey’s HSD multiple range test \((p > 0.05)\).

4. Discussion

The study of basic aspects that contribute to parasitoid–host interactions, such as the host age, density, and dispersal behavior, are necessary for determining parasitoid success potential [28] and in predicting the impact of parasitoids such as *S. endius* on the population dynamics of hosts, such as the fruit fly *B. cucurbitae*. Moreover, these data will be useful in calculating the pest host density, determining which parasitoid should be released in future biological control programs, and predicting the behavior of *S. endius* under different host population conditions.

The results of the current study indicated that female *S. endius* effectively parasitized its host, the fruit fly *B. cucurbitae*, at different ages (2, 4, and 6 days old), but the level of parasitism was the highest for 4-day-old *B. cucurbitae* pupae. The process of parasitization for a successful parasitoid–host relationship commonly consists of four steps: host habitat location, host location, host acceptance, and host suitability [29]. Host age is one of the major factors that affect host acceptance and host suitability of parasitoids, especially egg and pupal parasitoids [30]. Extensive histolysis of internal tissues in insect hosts predominates during the early pupal development of hosts, and histogenesis and differentiation of internal organs in hosts occur in the later pupal development of hosts [30–32]. Thus, older pupal hosts may contain fewer resources than younger pupal hosts to be used for the development of parasitoids. *Diadromus collaris* (Gravenhorst) preferred to parasitize *Plutella xylostella* (Linnaeus) when the host was in the first half of the pupal development [30]. Simple optimal diet theories predict that female parasitoids select hosts with higher nutritional quality to maximize their fitness return and foraging efficiencies [30,33].

We found increased parasitism of *S. endius* at high densities of *B. cucurbitae* pupae, which is in agreement with the finding on *B. dorsalis* pupae by Zhang et al. [28]. We also demonstrated an adverse effect of the increasing parasitoid density on the parasitism of *S. endius*. The host and parasitoid density could be the major factors influencing parasitic success.

Studies have found that soil conditions significantly influence the performance of parasitoids. It was observed in this study that no significant difference was noted in the parasitism rate of *S. endius* when the hosts were placed at soil depths between 0 and 1 cm, and *S. endius* could not parasitize *B. cucurbitae* pupae at soil depths of 4 cm and 5 cm under field conditions. These results are consistent with a previous study [34]. These might be due to the fact that the pteromalid parasitoid ovipositor is not long enough to be unable to reach its host at that depth. However, the soil depths of hosts did not affect the eclosion rate of *B. cucurbitae*. These findings indicate that *B. cucurbitae* might have evolved to adapt to deep soil conditions in order to escape parasitoid parasitism.

The releasing distance could significantly affect the parasitism rates of parasitoids [22,25,27,35,36]. In this study, we found that there was no significant difference in the parasitism rate of *S. endius* on *B. cucurbitae* pupae at distances of 0, 5, and 10 m. However, *Lysiphlebus curriui* (Marshall) successfully traveled up to 20 m to a new host patch of *Aphis*
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* fabae cirsiiacanthoides * Scopoli [22]. * Tetristichus julis * (Walker) females dispersed rapidly at least 600 m to find and parasitize the maturing beetle larvae of * Oulema melanopus * (L.) in newly planted wheat fields [37]. The percent parasitism by * Trichogramma chilonis * Ishii and * T. japonicum * Ashmead on * C. cephalonica * decreased with the increase in the releasing distance of 1 to 10 m, which had high and low parasitism at distances of 1 to 3 m and 8 to 9 m, respectively [25]. * S. cameroni * could parasitize 46.9% of the total parasitism at 1 m but only caused 9.9% of the total parasitism at 10 m [27]. Thus, the dispersal ability of parasitoids varies among different species of parasitoids, hosts, and crop species.

5. Conclusions

Our study found that increasing host densities improved the parasitism of * S. endius * to * B. cucurbitae * pupae, and the age of * B. cucurbitae * pupae did not affect the parasitism and the progeny sex ratio of * S. endius *.

*S. endius * density significantly influenced the total parasitism of * S. endius * against * B. cucurbitae * pupa and * B. cucurbitae * mortality. No significant differences in the emergence rates and sex ratio of * S. endius * were found in relation to parasitoid densities. Different depths of * B. cucurbitae * pupae in soil significantly affected the parasitism and eclosion rates of * S. endius *.

No significant difference in the parasitism rate of * S. endius * was observed across different releasing distances. These results may provide a theoretical basis for the release strategies of * S. endius * against other hosts. Future studies could also evaluate the performance and parasitic efficiency of * S. endius * on * B. cucurbitae * in different crop systems under laboratory and field conditions.

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