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Interspecific competition between *Snellenius manilae* and *Meteorus pulchricornis*, larval parasitoids of *Spodoptera litura*

W.-T. Chen and S.-Y. Hwang*

Department of Entomology, National Chung Hsing University,
Taichung, Taiwan

Abstract

Snellenius manilae (Ashmead) and *Meteorus pulchricornis* (Wesmael) (Hymenoptera: Braconidae) are larval endoparasitoids of *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae). Both species preferentially parasitize early-instar *S. litura* and occupy similar ecological niches. Therefore, competition between the two species may occur. In this study, intrinsic competition and cage experiments were conducted to discuss the interactions between *S. manilae* and *M. pulchricornis*. The results indicated that in intrinsic competition, *M. pulchricornis* was always the dominant species. In cage experiments, when the total number of parasitoids was four, the parasitism rates following the release of one species were significantly higher than the release of two species simultaneously. In addition, parasitism rate of eight *M. pulchricornis* was also significantly higher than the parasitism rate of the treatment released four *S. manilae* and four *M. pulchricornis* simultaneously. Therefore, competition occurs between *S. manilae* and *M. pulchricornis*, and *M. pulchricornis* is typically the superior of the two species. The use of *M. pulchricornis* as a biological agent for *S. litura* should be considered.

Keywords: interspecific competition, intrinsic competition, *Meteorus pulchricornis*, *Snellenius manilae*, *Spodoptera litura*

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Introduction

The natural population of insect herbivores can be controlled using various natural enemies. Typically, natural enemies share hosts with minimal competition because of temporal or spatial separation. However, field surveys have revealed that more than one natural enemy species can exist simultaneously, and that these coexisting natural enemies might compete for limited resources (Harvey *et al.*, 2013). Predators are predominantly generalists and can switch to alternative prey to avoid competition. Parasitoids tend to be specialists with a narrow host range. Competition can occur when more than one parasitoid species occupies the same host population, particularly when two solitary endoparasitoid species occupy similar niches simultaneously. The co-occurring endoparasitoid species might oviposit successively on the same host but, typically, only one endoparasitoid offspring can survive and become cocooned (De Moraes *et al.*, 1999; Tamò *et al.*, 2006; Cingolani *et al.*, 2013). Therefore, past studies have suggested some substantial competition that might occur between endoparasitoid species.

In endoparasitoid species, two types of competition can occur: intrinsic and extrinsic competition. Intrinsic competition occurs inside the host body at the parasitoid larval stage. By contrast, extrinsic competition occurs between adult parasitoids outside the host body (Mills, 2006; Harvey *et al.*, 2013). Competitive interaction can affect the population size, development time, survival rate, and individual size of the competing parasitoid species (Price *et al.*, 1988; Reitz, 1996; Bogran *et al.*, 2002; Tian *et al.*, 2008). Moreover, competition among the natural enemies might even decrease the control efficiency of one specific species or the sum efficiency. For example, when

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*Author for correspondence
Phone: +886-4-22840363
Fax: +886-4-22875024
E-mail: oleander@dragon.nchu.edu.tw

Campoletis chlorideae (Uchida) and *Eriborus argenteopilosus* (Cameron) (Hymenoptera: Ichneumonidae) are released concurrently, the parasitism rate of *E. argenteopilosus* is lower than it is when they are released individually (Bajpai *et al.*, 2006). Tamò *et al.* (2006) similarly reported that *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae) and *Campoletis sonorensis* (Cameron) (Hymenoptera: Ichneumonidae) exhibit higher parasitism rates when released separately than when released concurrently.

Spodoptera litura (Fabricius) (Lepidoptera: Noctuidae) is a polyphagous insect pest of several crops. A study recorded 389 plant species belonging to 109 families that are host plants of *S. litura* (Qin *et al.*, 2006). Although this insect has caused substantial economic damage in numerous countries, it reportedly has several natural enemy species. Ranga Rao *et al.* (1993) indicated that *S. litura* may contain as many as 71 species of parasitic enemy species worldwide. Field surveys have identified 14 parasitoid species of *S. litura* in Taiwan (Chiu & Chou, 1976; Chen *et al.*, 2009). Because parasitoid species are highly diverse, they can become valuable resources for the biological control of *S. litura*.

Snellenius manilae (Ashmead) (Hymenoptera: Braconidae) is the most common and widely distributed solitary endoparasitoid of *S. litura* larvae in Taiwan (Chiu & Chou, 1976). All recorded hosts of *S. manilae* belong to the *Spodoptera* genus (Rajapakse *et al.*, 1985; Lu, 1989; Ando *et al.*, 2006; Sun & Huang, 2010; Qiu *et al.*, 2012), in which the *S. manilae* parasitoid is the dominant species. In addition, *Meteorus pulchricornis* (Wesmael) (Hymenoptera: Braconidae) is a solitary *S. litura* endoparasitoid species first reported to parasitize *S. litura* in Taiwan in 1976 (Chiu & Chou, 1976). One study identified two strains of *M. pulchricornis*: an arrhenotokous (biparental) group from Europe and a thelytokous (uniparental) group from Asia (Fuester *et al.*, 1993). The host range of *M. pulchricornis* consists of 11 families of Lepidoptera (Huddleston, 1980; Okada, 1989; Maetô, 1990; Berry, 1997).

S. manilae and *M. pulchricornis* are both solitary endoparasitoids of *S. litura*. During a field survey, both species can be identified in the same location at the same time. Studies have indicated that *S. manilae* and *M. pulchricornis* prefer to parasitize second- or third-instar *S. litura* larvae (Qiu & Tang, 2010; Chen *et al.*, 2011). Therefore, because of niche overlap, a competitive relationship may exist between the two species. However, according to our research, no study has reported a competitive interaction between these two parasitoid species. Therefore, the objective of this study was to evaluate the competition between *S. manilae* and *M. pulchricornis* when *S. litura* was used as the host.

Materials and methods

Plant

Brassica oleracea was used as the host plant in all experiments. Seeds were purchased from Know-You Seed Co., Ltd, and commercial soil (Stender, Germany) was used to cultivate these plants. To sterilize the seed surface and accelerate germination, the seeds were placed in a water bath at 45°C for 30 min before they were sown (Yadav *et al.*, 2010). After warm-water treatment, the seeds were sown into a $30 \times 20 \times 5$ cm^3 plastic plate. After 1 week, the plantlets were separately transplanted to 4-inch pots. All plants were cultivated in a greenhouse at 25 ± 2°C in a light-dark (LD) 16:8 h cycle.

Host

The initial population of *S. litura* was collected from a field in Caohu, Dali District, Taichung City, Taiwan. The population was maintained in incubators at 25 ± 2°C, in an LD 12:12 h cycle at 70 ± 5% relative humidity (RH). The *S. litura* larvae were provided an artificial diet adopted from Kao (1995), reared in plastic cups (8 cm diameter × 6 cm height) until the sixth instar, and then transferred to separate wells in 30-well plates until pupation. Pupae were collected and placed into plastic cups and were then sterilized using a 25% bleaching liquid (Clorox). Adult *S. litura* were placed in a plastic cylinder (14.9 cm diameter × 21 cm height), and tissue paper was used to cover the inside to facilitate the collection of eggs. The plastic cylinders were maintained in laboratory conditions and the adult moths were provided a sugar solution (Kao, 1995; Yadav *et al.*, 2010). The egg masses were collected, placed into plastic cups, and sterilized using 1.5% sodium hypochlorite (Riedel-de Haën). According to previous studies (Ando *et al.*, 2006; Qiu & Tang, 2010; Chen *et al.*, 2011), *S. manilae* and *M. pulchricornis* prefer to parasitize early instars of *S. litura*; therefore, second-instar larvae were used in the bioassays.

Parasitoids

S. manilae and *M. pulchricornis* were obtained from parasitized *S. litura* larvae collected from the field. Both parasitoids were reared in incubators at 25 ± 2°C in an LD 12:12 h cycle at 70 ± 5% RH. Second-instar *S. litura* larvae were used as the host for the parasitoids. Parasitized *S. litura* were provided an artificial diet and kept in plastic cups. After parasitoid larvae emerged from the hosts and became cocooned, the cocoons were collected and placed in petri dishes (5.5 cm diameter × 1.5 cm height; Alpha Plus Scientific Corp). Adults were transferred to a plastic cup and provided a 15% (w/w) sugar solution . According to the previous studies about the fecundity peak of the two parasitoids (Hwang *et al.*, 2010; Ting, 2011), *S. manilae* aged 3–5 days and *M. pulchricornis* aged 13–15 days were used in bioassays.

Intrinsic competition

Various sequences and time intervals were used to evaluate the intrinsic competition between *S. manilae* and *M. pulchricornis* inside *S. litura* body. Second-instar *S. litura* larvae were fed on 29-day-old *B. oleracea* for 24 h and then prepared for the test. The larvae were first parasitized by one parasitoid species and then, after the specific time intervals, were parasitized by the other parasitoid species. The specific time intervals were 0, 6, 12, 18, 24, and 48 h. Overall, 12 treatments were tested. The *S. litura* larvae were verified to have been successfully parasitized when they were stung by the parasitoid ovipositor. Each replication of treatments comprised 30 trials, and each treatment was replicated five times. Parasitized *S. litura* larvae were maintained in individual petri dishes and provided an artificial diet. When the parasitoids emerged to cocoon, the species of parasitoids were recorded.

Cage experiments

In the cage experiments, different numbers of the two parasitoid species were evaluated. Second-instar *S. litura* larvae ($n = 120$) were transferred into a $30 \times 30 \times 30$ cm^3 cage

(MegaView Science Co, Ltd) and fed 29-day-old *B. oleracea* for 24 h. Different numbers of two different parasitoid species were then released into the test cage. In each treatment, four or eight parasitoids, either *S. manilae* or *M. pulchricornis*, or a combination of both species, were used. After 24 h of exposure, the *S. litura* larvae were transferred into individual petri dishes and provided an artificial diet until the parasitoids emerged. For each treatment, the parasitoid species of cocoons and the parasitism rate were recorded and five replications were conducted.

Data analysis

The cocoons collected from each treatment of intrinsic competition were separated by parasitoid species and the cocoon ratios of *S. manilae* and *M. pulchricornis* were calculated. In cage experiments, the parasitism rates were estimated based on the number of cocoons and the number of unparasitized hosts. Furthermore, the cocoons collected from the treatments involving both parasitoids were separated by parasitoid species and calculated to ratio values. All data collected from each experiment were analyzed by SAS version 9.00 and were subjected to χ^2 test. In the cage experiments, pairwise comparisons with Bonferroni corrections between treatments were conducted in the case of significance.

Results

Intrinsic competition

Our results indicated that, when *M. pulchricornis* was the first parasitoid to parasitize, significantly greater *M. pulchricornis* than *S. manilae* cocoons were collected regardless of the ovipositional intervals between the two parasitoids (fig. 1). *M. pulchricornis* cocoon ratios were consistently higher than 75% in all treatments. However, when *S. manilae* was the initial parasitoid, the competitive outcomes depended on the interval of time between two parasitization (fig. 2). The cocoon ratios of *S. manilae* increased as the time between two parasitization increased, whereas the cocoon ratios of *M. pulchricornis* decreased as the time between two parasitization increased. In the treatments involving 0 and 6 h time intervals, the cocoon ratios of *M. pulchricornis* were 71 and 69%, respectively. The cocoon numbers of *M. pulchricornis* were significantly higher than those of *S. manilae* ($\chi^2 = 19.59$, $P < 0.0001$; $\chi^2 = 16.04$, $P < 0.0001$). When the time intervals between the first and second parasitization were 12 and 18 h, no significant difference between the two parasitoids was observed ($\chi^2 = 0.43$, $P = 0.5102$; $\chi^2 = 2.06$, $P = 0.1508$). When the time intervals were longer than 24 h, *S. manilae* cocoons were significantly more than *M. pulchricornis* cocoons. The cocoon ratios of *S. manilae* were 66 and 84% for 24 and 48 h intervals, respectively.

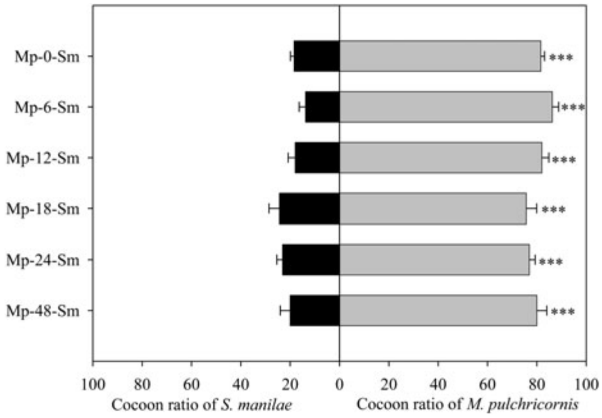

Fig. 1. Cocoon ratios (Mean + SE) of *M. pulchricornis* (Mp) and *S. manilae* (Sm) when *M. pulchricornis* was the first to oviposit in host larvae of *S. litura*, followed by *S. manilae* at different time intervals. The numbers between Mp and Sm are the time intervals (h) between the two parasitizations. The asterisks indicate a significant difference between the two parasitoids within each time interval (χ^2: *** $P < 0.0001$).

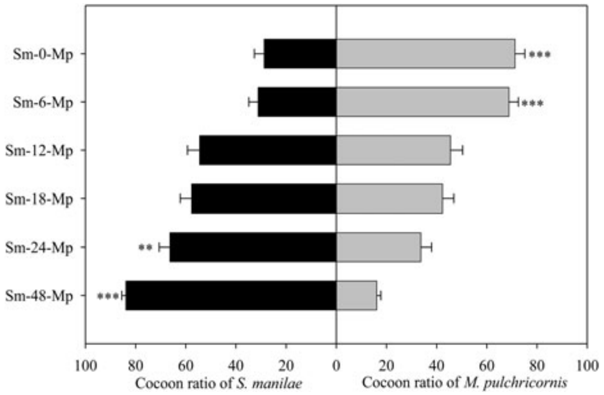

Fig. 2. Cocoon ratios (Mean + SE) of *M. pulchricornis* (Mp) and *S. manilae* (Sm) when *S. manilae* was the first to oviposit in host larvae of *S. litura*, followed by *M. pulchricornis* at different time intervals. The numbers between Mp and Sm are the time intervals (h) between the two parasitizations. The asterisks indicate a significant difference between the two parasitoids within each time interval (χ^2: $^{**}P < 0.01$ and $^{***}P < 0.0001$).

Cage experiments

The results of cage experiments indicated that parasitism rates increased with parasitoids density. The parasitism rates were significantly higher in the treatments of eight parasitoids than that in the treatments of four parasitoids whether *M. pulchricornis* only, *S. manilae* only, or both species were released together ($\chi^2 = 25.55$, $P < 0.0001$; $\chi^2 = 35.33$, $P < 0.0001$; $\chi^2 = 76.51$, $P < 0.0001$). The parasitism rates by *M. pulchricornis* only were not significantly different from that by *S. manilae* only in both densities (fig. 3). When both parasitoid species were released together, the total parasitism rates reduced at each parasitoid density. Following the release of four parasitoids, the parasitism rates by only one parasitoid species were significantly higher than that by two species released together ($\chi^2 = 50.97$, $P < 0.0001$, fig. 3a). Similarly, following the release of eight parasitoids, the parasitism rate by *M. pulchricornis* only was significantly higher than that by two species released together ($\chi^2 = 8.81$, $P = 0.0122$, fig. 3b). When both parasitoid species were released together, the cocoon numbers of *M. pulchricornis* were significantly higher than that of *S. manilae* (fig. 4). In the treatment involving two *M. pulchricornis* and two *S. manilae* parasitoids, *M. pulchricornis* cocoon ratio accounted for 57% of all cocoons ($\chi^2 = 5.65$, $P = 0.0174$,

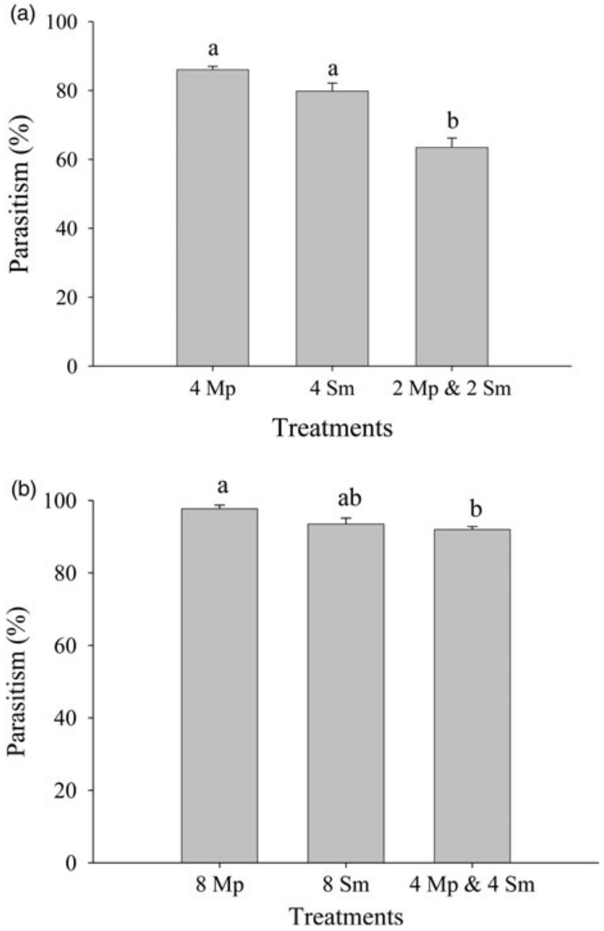

Fig. 3. Parasitism rates (Mean + SE) obtained from different treatments when the total number of female parasitoids was (a) four or (b) eight in cage experiments. Mp: *M. pulchricornis*; Sm: *S. manilae*. The same letter above bars indicates no significant difference among treatments (χ^2 with Bonferrini correction, $P < 0.05$).

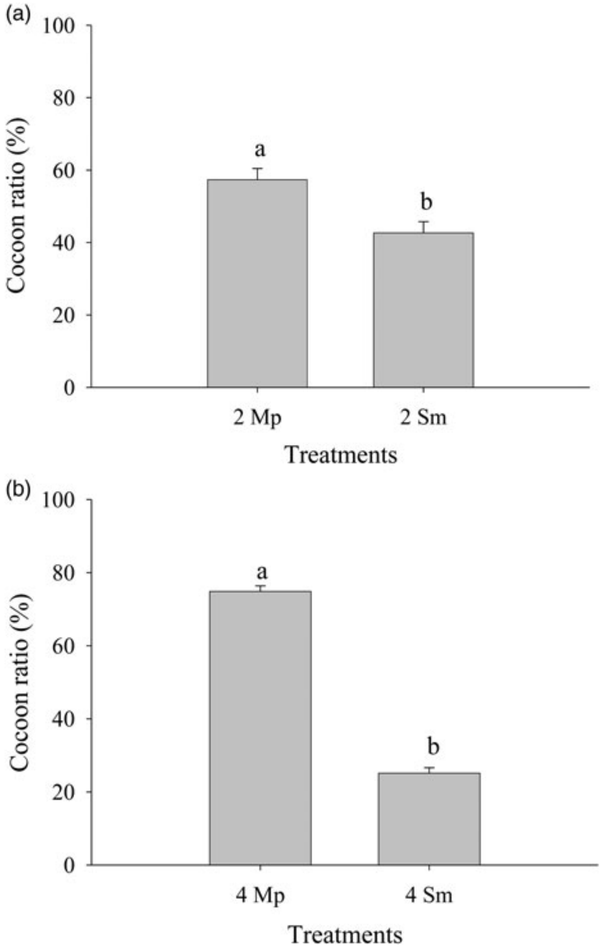

Fig. 4. Cocoon ratios (Mean + SE) of *M. pulchricornis* (Mp) and *S. manilae* (Sm) in (a) the treatment released two *M. pulchricornis* and two *S. manilae* and (b) the treatment released four *M. pulchricornis* and four *S. manilae*. Different letters above bars indicate significant differences between the ratios of *M. pulchricornis* and *S. manilae* (χ^2: $P < 0.05$).

fig. 4a). In the treatment in which four *M. pulchricornis* and four *S. manilae* parasitoids were released, *M. pulchricornis* cocoon ratio accounted for 75% of all cocoons ($\chi^2 = 66.50$, $P < 0.0001$, fig. 4b). More *M. pulchricornis* cocoons emerged than those of the *S. manilae* indicated the superiority of *M. pulchricornis*. Furthermore, the difference of the cocoon numbers between *M. pulchricornis* and *S. manilae* increased with parasitoids density.

Discussion

Our results indicated that competition occurred between *S. manilae* and *M. pulchricornis* when these two wasps parasitized *S. litura* simultaneously. In the majority of the tested conditions, *M. pulchricornis* was the dominant parasitoid. However, these results contrast the findings of previous field surveys in which *S. manilae* was the dominant of the two species (Chiu & Chou, 1976).

Previous studies have indicated that the duration of the egg stage may be the principal factor determining the success of a parasitoid in intrinsic competition because the first-hatching species can use the host's resources immediately and attack the eggs of the other parasitoids (Tillman & Powell, 1992; Bajpai *et al.*, 2006; Tian *et al.*, 2008). Qiu *et al.* (2012) reported that the eggs of *S. manilae* hatched in approximately 2.7 days (26°C, LD 14:10 h) when second-instar *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) was the host. When *M. pulchricornis* was observed to parasitize *Mythimna separata* (Walker) (Lepidoptera: Noctuidae), the egg period was approximately 3.8 days (25 ± 1°C, LD 16:8 h) (Magdaraog *et al.*, 2012). The observation of our study similarly indicated that *M. pulchricornis* egg-larva stage required a longer developmental period than *S. manilae*. According to the hatching time, *S. manilae* should be the prevailing parasitoid when *S. manilae* and *M. pulchricornis* exist inside a host body concurrently. However, our results indicated that, when *S. manilae* and *M. pulchricornis* parasitized *S. litura* larvae simultaneously, *M. pulchricornis* was the dominant species unless *S. manilae* parasitized *S. litura* at least 12 h prior to *M. pulchricornis*.

Therefore, traits other than the hatching sequence may play major roles in determining the fates of the competing parasitoids.

To protect the eggs from encapsulation of the host immune system, parasitoid females will inject either the venom, calyx fluid, polydnavirus (PDV), non-PDV symbiotic viruses, or virus-like particles into the host body (Pennacchio & Strand, 2006). Adult *M. pulchricornis* has been reported to release virus-like particles into the host body during oviposition. These chemical particles can protect the parasitoid egg from host encapsulation by inhibiting the spread of granulocytes and plasmatocytes as well as the induction of apoptosis (Suzuki & Tanaka, 2006; Suzuki *et al*., 2008, 2009). In addition, *S. manilae* was reported having polydnsvirus symbiont which could prevent the encapsulation from the host (Sri Ratna *et al*., 2011). The abilities of these two parasitoids to avoid encapsulation can affect not only the success of parasitization but also the results of interspecific competition. Furthermore, the virulence released by parasitoid females may also have the effect on the parasitic competitors. Besides chemical effects, Magdaraog *et al*. (2012) and Chau & Maeto (2008) indicated that *M. pulchricornis* larvae possess large mandibles and retain a caudal appendage. *M. pulchricornis* larvae might use the mandibles to attack competitors and the caudal appendage to move in the host body. Suzuki & Tanaka (2007) indicated that the *M. pulchricornis* embryo is enclosed in a serosal cell membrane that might protect the parasitoid from defensive reactions of the host. These physical characteristics might also contribute to the superiority of *M. pulchricornis* in intrinsic competition.

The cage experiments results indicated that treatment combining *S. manilae* and *M. pulchricornis* is associated with the lowest parasitism rate. This observation indicated that direct competition or interference occurs when the two parasitoid species exist in the same place at the same time. Similarly, Tamò *et al*. (2006) identified lower parasitoid cocoon numbers following the concurrent release of *C. marginiventris* and *C. sonorensis* in comparison with the separate release of the species.

Following the simultaneous release of *M. pulchricornis* and *S. manilae* in the bioassay, we collected a significantly higher number of *M. pulchricornis* cocoons than *S. manilae* cocoons from the parasitized *S. litura* larvae. This result was expected because *M. pulchricornis* dominated the intrinsic competition and, thus, cocoons emerging from the host body were more likely to be *M. pulchricornis* than *S. manilae*. Previous studies similarly observed that *C. chlorideae* and *C. sonorensis* were the dominant parasitoids in intrinsic competition and contributed higher numbers of cocoons when they were released with other parasitoids (Bajpai *et al*., 2006; Tamò *et al*., 2006). Our study results indicated that the parasitism rate increased as the number of parasitoids released increased, and might increase by up to 100% following the release of more than eight parasitoids.

According to our results, *M. pulchricornis* is substantially more competitive than *S. manilae* in intrinsic competition and cage experiments. However, previous studies have indicated that *S. manilae* is the prevailing parasitoid of *S. litura* in Taiwan (Chiu & Chou, 1976). The reason for the discrepancies in results is unclear. *M. pulchricornis* may have several properties that facilitate the control of *S. litura*, such as thelytoky, ease of mass propagation, and the longer adult longevity (Ando *et al*., 2006; Hwang *et al*., 2010). Therefore, additional studies are required to fully elucidate the potential of using *M. pulchricornis* as a biological agent for controlling *S. litura*.

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