

# Host adaptation of a gregarious parasitoid *Sclerodermus harmandi* in artificial rearing

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**Abstract** Adaptations of a parasitoid, *Sclerodermus harmandi* (Buysson 1903) (Hymenoptera: Bethyridae) to a target host, *Monochamus alternatus* Hope (Coleoptera: Cerambycidae), were investigated in laboratory colonies. We quantified the physiological and behavioral flexibility of the parasitoid reared on *M. alternatus* compared to the parasitoid reared on a common host, *Saperda populnea* (Coleoptera: Cerambycidae). Adult performance (fecundity and pre-oviposition period) and offspring physiological responses (mortality and sex ratio) of *S. harmandi* reared on *M. alternatus* improved over multiple generations. *S. harmandi* females of the 12th generation on the target host showed better performance, i.e., shorter time for searching and handling, higher oviposition preference, and, subsequently, lower offspring mortality and proportion of male emergence on the host than those from the base stock. Our work demonstrated that these traits in *S. harmandi* were influenced by the integration of cultured generations and host quality, which implies that the potential

effectiveness of *S. harmandi* as a biological control agent can be further improved.

**Keywords** Biological control · Hymenoptera · Bethyridae · Behavioral flexibility · Physiological response · Successive generations · Sex allocation

## Introduction

The success of biological control with inundative releases of parasitoids depends, in part, on an efficient mass-rearing system for the parasitoids, producing large numbers of parasitoids of high quality (Chambers 1977; Gandolfi et al. 2003). A vast amount of research has examined mass-rearing techniques of parasitoids (Pérez-Lachaud and Hardy 2001; Shimoji and Miyatake 2002). At times, artificial rearing can have some negative effects on host searching and parasitization rates of parasitoids (Chambers 1977; Gandolfi et al. 2003). Such effects may be a consequence of behavioral or physiological alterations of parasitoids arising when parasitoids are reared on a substitute host rather than the target host (Gandolfi et al. 2003; Shimoji and Miyatake 2002; Henry et al. 2008).

*Sclerodermus harmandi* (Buysson, 1903) (Hymenoptera: Bethyridae) is one of the most common biocontrol agents attacking young stage larvae and

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pupae of *Monochamus alternatus* Hope (Coleoptera: Cerambycidae), a primary vector of the pinewood nematode, *Bursaphelenchus xylophilus* (Steiner et Buhner) Nickle. The bethylid was regarded as *Scleroderma guani* Xiao and Wu (Xiao and Wu 1983), used widely for the control of cerambycid larvae in the forests of China, and was revised as the junior synonym of *S. harmandi* (Buysson, 1903) (Terayama 1999; Lim et al. 2006; Xu and He 2008). Consequently, *S. harmandi* is of particular interest to researchers in China (Zhang 1980; Qin et al. 1982; Xu et al. 2008), with considerable research focused on the biological control of *M. alternatus* by parasitoids (Shimazu et al. 1995; Yang 2004). *S. harmandi* is an idiobiont parasitoid which permanently paralyzes the hosts prior to feeding and oviposition. Thus, it is generally used to control first–third instar larvae of *M. alternatus* with lower behavioral defense. To that end, the primary tactic has been periodic field releases of large numbers of parasitoids mass-reared in the laboratory. To date, mass-rearings of *S. harmandi* have utilized the larvae of a common host, *Saperda populnea* (Cerambycidae: Lamiinae), largely because of its availability and a habit of non-cannibalism. However, alternation from other culturing hosts to target hosts may impact the parasitic potential of parasitoids, sometimes even deteriorating with generations reared. To date, there has been little consideration on the quality of mass-reared parasitoids in terms of behavioral and biological performance. Monitoring adaptive changes in life history traits throughout the reared generations plays an important role in the quality control of mass-rearing insects (Chambers 1977). Therefore, evaluation of the parasitic potential of *S. harmandi* mass-rearing on the target host is a prerequisite for successful application in the field.

The objective of this study was to investigate how the biological and behavioral adaptations of the parasitoid *S. harmandi* can be rapidly shaped to a target host. We successively reared *S. harmandi* on a target host for 12 consecutive generations and evaluated the performance of *S. harmandi* reared on the substitute and target host. Effects of the interactions between generations and host quality on the parasitoid's fitness consequences (adult and offspring performance) were examined.

## Materials and methods

### Experimental insects

Parasitoids, *S. harmandi* reared on *S. populnea* were provided by the Xishan Forest Farm, Beijing, China, and used as the base stock for laboratory colonies on the larvae of *M. alternatus* (Ma colony) and on the mature larvae of *S. populnea* (Sp colony) for our laboratory experiments for 12 successive generations. Parasitoids were reared individually in a vial (7.5 cm in height  $\times$  1.2 cm in diameter), blocked with a tampon on the port, kept at  $25 \pm 5^\circ\text{C}$ , 70% relative humidity, under a light–dark (LD) cycle of 14:10 h. The third instar larvae of *M. alternatus* were collected from trees within the pine wilt nematode-affected zone in Zhejiang province, China. All third instar larvae of hosts were stored at  $8\text{--}10^\circ\text{C}$  prior to use in parasitoid rearing.

### Performance test for successive generations on the target host

Sixty mated females (five days old:  $F_0$  generation) from the base stock (Sp colony) were reared on the larvae of *M. alternatus*. Mated female *S. harmandi* were fed on 10% honey for 5–6 days to ensure oogenesis and then presented with host larvae in each pipe for subsequent ovipositioning/feeding. For the colony reared on *M. alternatus*, the larvae were presented at a ratio of 3:1 parasitoid/host, whereas a ratio of 3:4 parasitoid/host was used for those reared on *S. populnea*, due to differences in larval weight between the two species. The mean weight of one *M. alternatus* larva is equal to four *S. populnea* larvae (Zhang 2004). Generation times for *S. harmandi* were approximately 35 days on *M. alternatus* and 25 days on *S. populnea*. Female adults ( $F_0$ ) were allowed to feed and reproduce on the hosts. Newly emerged male and female wasps ( $F_1$ ) were allowed to mate freely and fed 10% honey in the vial. After five days, females were randomly moved into other new pipes with host larvae at the same inoculation rate (described above). The same procedure was followed as before for each generation with 20 replicates and continued for 12 generations. Simultaneously, the parasitoids of Sp colony from  $F_1$  to  $F_{12}$  were maintained as controls. We recorded the performance of the two strains for each generation, including adult

fecundity (the number of eggs laid per female), pre-oviposition and oviposition period (days), development rate ( $\text{days}^{-1}$ ), mortality, and sex ratio (proportion of males). The pre-oviposition periods of adult females were counted as the time from emergence to first reproduction in females (APOP) (Gabre et al. 2005).

#### Adaptation to the target host

No-choice experiments were conducted in vials blocked with a tampon on the port (as mentioned above). Twenty-five female wasps ( $F_{12}$ ) of Ma and Sp colonies were chosen randomly from each colony to compare their behavioral alteration (searching and handling time) and subsequent fitness measures (fecundity, mortality, and sex ratio) on target hosts and on substitute hosts, respectively. A single mated female parasitoid of 4–5 days old was allowed to search and handle the host (a larva of *M. alternatus* or *S. populnea*) within each vial. After 5 min, we started to record the searching time by the individual wasp to detect hosts from the start of walking to first landing and probing on the hosts and handling time for paralyzing hosts, until the hosts were not active any more (Morrison and Lewis 1981). Adult and offspring fitness consequences on each host were recorded after the female wasps oviposited and offspring completed development on the paralyzed hosts for 30–40 days. Deteriorated hosts were replaced and mortality was checked daily.

A two-choice test was used to determine the oviposition preference of  $F_{12}$  females from both the Ma and Sp colonies. Five-day-old female wasps ( $F_{12}$ ) were employed in the bioassay with one larva of the two host species offered simultaneously in a glass Petri dish (12 cm in diameter). Five female wasps were released on the center of each dish with a fine brush. A total of 25 female wasps were used for each treatment with five replicates. The experiments were conducted at 25–26°C under a lamp (45 W) hanging approximately 0.5 m above the roof over the experimental arena. We recorded the oviposition preference of parasitoids in the Petri dish, which lasted for two weeks until the female did not lay any more eggs. The oviposition preference of parasitoids was expressed as the number of eggs per female on host per weight (mg) in order to correct for differences in host size.

#### Data analysis and statistics

The biological fitness parameters of adults, offspring, and the oviposition preference were analyzed with the *t*-test. Two-way analysis of variance (ANOVA) was used to compare the fitness (fecundity, pre-oviposition and oviposition periods, mean development rate, mortality, and sex ratio) among colonies and generations. Except for the percentage-based data (mortality and sex ratio), which followed arcsine square root transformation, logarithm transformation of the data was performed prior to the analysis. All statistical analyses for this study were performed using SPSS 13.0 for Windows (SPSS Inc., Chicago, IL, USA).

## Results

#### Performance test for successive generations

There was a significant correlation among generations, hosts, and fitness consequences (Table 1). Adult fecundity was explained primarily by the number of generations in culture and the interaction between the generation number and host species. Both generations in culture and host species significantly affected the duration of pre-oviposition and oviposition (Table 1). The development rate of offspring depended on the number of generations in culture, host species, and interaction between them (Table 1). The mortality of offspring was due to the effects of generations in culture. Variances in the offspring sex ratio were significantly determined by host species (Table 1).

The adult fecundity of *S. harmandi* increased linearly over 12 generations on the target host, *M. alternatus*, and the substitute host, *S. populnea* (Fig. 1a;  $y = 3.1197x + 21.77$ ,  $r = 0.772$ ,  $P < 0.001$ ;  $y = 1.3874x + 32.007$ ,  $r = 0.7553$ ,  $P < 0.001$ , respectively). However, the mean number of eggs laid by each female was significantly higher on *M. alternatus* than on *S. populnea* after culturing for six generations (Fig. 1a). The mean pre-oviposition period on *M. alternatus* was 12.2 days, approximately 3.0 days more than on *S. populnea* (Fig. 1b). The mean duration of oviposition on *M. alternatus* was 5.3 days during the first three generations in culture, but was 6.7 days during the last five generations.

**Table 1** Analysis of variance for interactive effects of generations and hosts on the average fitness consequences of 12 successive generations of *Sclerodermus harmandi* on different hosts (ANOVA,  $n = 25$  in each treatment)

Source	SS	df	F	P
Adult performance fecundity (eggs per female)				
Generation	3.895	11	41.170	<0.001
Host	0.000	1	0.036	0.850
Generation × host	0.669	11	7.074	<0.001
Error	3.922	456		
Pre-oviposition period (days)				
Generation	0.300	11	11.742	<0.001
Host	1.648	1	708.555	<0.001
Generation × host	0.026	11	1.014	0.433
Error	1.061	456		
Oviposition period (days)				
Generation	0.929	11	9.910	<0.001
Host	3.430	1	402.512	<0.001
Generation × host	0.275	11	2.939	0.001
Error	3.885	456		
Offspring performance development rate (days <sup>-1</sup> )				
Generation	0.003	11	9.738	<0.001
Host	0.030	1	1,034.414	<0.001
Generation × host	0.012	11	37.618	<0.001
Error	0.013	456		
Mortality (%)				
Generation	3.996	11	15.128	<0.001
Host	0.086	1	3.583	0.059
Generation × host	0.510	11	1.930	0.034
Error	10.949	456		
Sex ratio (% male)				
Generation	0.057	11	2.079	0.021
Host	0.265	1	107.174	<0.001
Generation × host	0.016	11	0.575	0.850
Error	0.821	456		

During F<sub>4</sub> to F<sub>7</sub>, the mean duration of oviposition increased significantly to 7.6 days (Fig. 1c).

The mean development rate of *S. harmandi* on *M. alternatus* was always quicker than on *S. populnea* after the second generation, but there were no significant differences among culturing generations (Fig. 1d). As a whole, the offspring mortality of F<sub>1</sub> and F<sub>2</sub> varied greatly from 49.98% to 20.32%, with an average level of 13.80% from F<sub>3</sub> to F<sub>12</sub> (Fig. 1e). Female wasps had a lower proportion of male

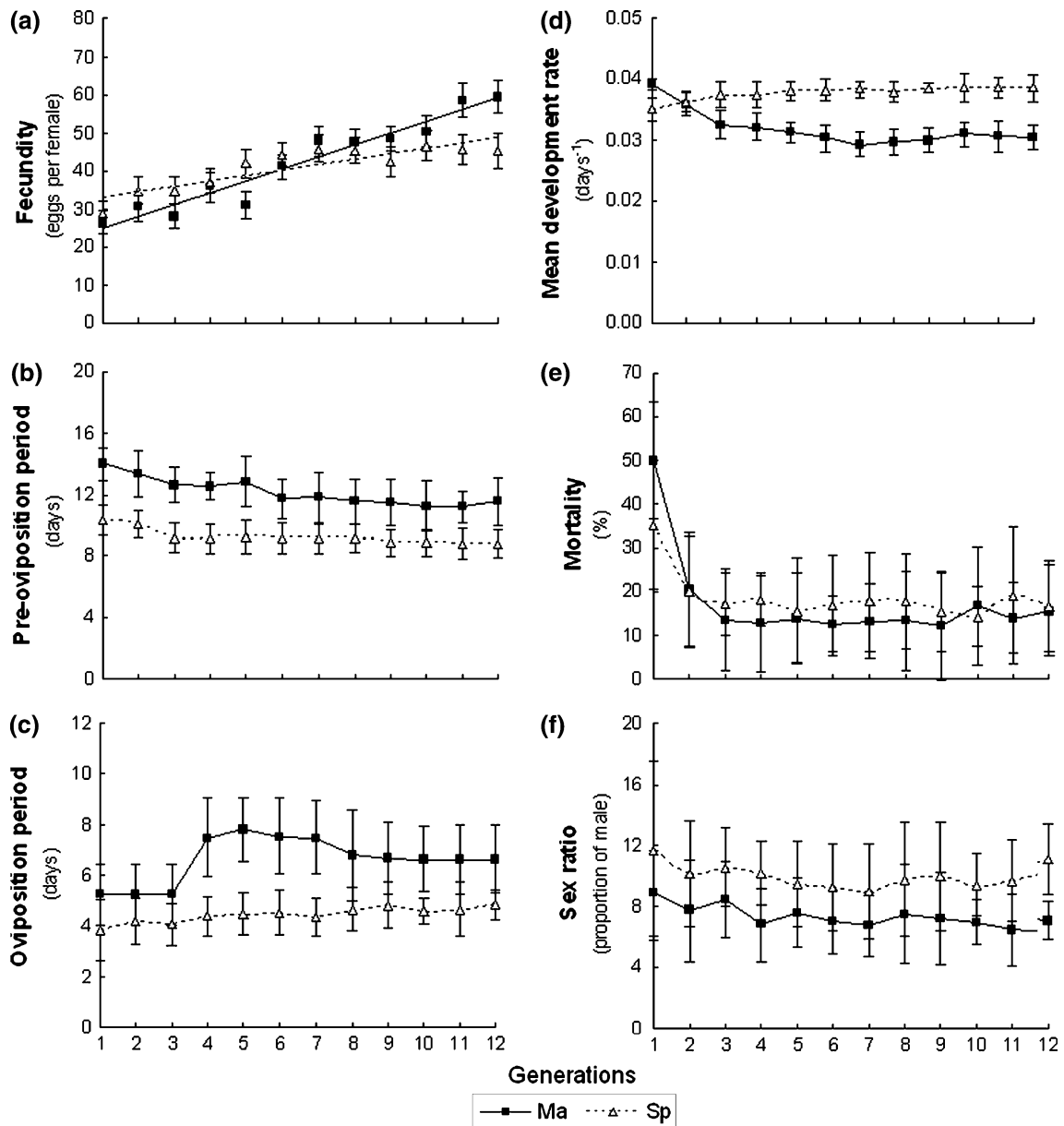
offspring on *M. alternatus* than on *S. populnea*, regardless of generations (Fig. 1f).

#### Adaptation to the target host

There was a significant correlation among colonies, host quality, and fitness consequences (Table 2). Searching time and oviposition preference was explained primarily by host species and the interaction between host species and colonies (Table 2). Handling time and offspring mortality were dependent on colonies, host species, and interaction between them (Table 2). The offspring sex ratio was significantly determined by host quality (Table 2).

Female wasps from the F<sub>12</sub> generation of the Ma colony spent much less time searching and handling the *M. alternatus* than females from the Sp colony (Fig. 2a, b; searching time,  $t_{38} = -6.812$ ,  $P < 0.001$ ; handling time,  $t_{38} = -5.760$ ,  $P < 0.001$ ). However, females from the Ma colony spent more time searching and handling *M. alternatus* than searching and handling *S. populnea* (Fig. 2a, b; Ma,  $t_{38} = 3.055$ ,  $P = 0.004$ ; Sp,  $t_{38} = 7.807$ ,  $P < 0.001$ ). Female wasps of the Ma colony (F<sub>12</sub>) oviposited more frequently on *M. alternatus* than on *S. populnea* (Fig. 2c;  $t_{38} = 8.454$ ,  $P < 0.001$ ). The mean number of eggs laid on *M. alternatus* (per weight [mg]) by individual females was  $0.467 \pm 0.092$  for Ma females and  $0.194 \pm 0.040$  for Sp females. In contrast, F<sub>12</sub> females of the Sp colony laid fewer eggs on *M. alternatus* than on *S. populnea* (Fig. 2c;  $t_{38} = 11.333$ ,  $P < 0.001$ ).

There were significant differences in the mortality of Ma and Sp colonies on *M. alternatus* (Fig. 3a;  $t$ -test:  $t_{38} = -9.118$ ,  $P < 0.001$ ), but not on *S. populnea* (Fig. 3a;  $t$ -test:  $t_{38} = 0.140$ ,  $P = 0.889$ ). The offspring mortality of the Ma colony (F<sub>12</sub>) did not differ between the two host species (Fig. 3a;  $t$ -test:  $t_{38} = -0.715$ ,  $P = 0.479$ ). However, the offspring of the Sp colony (F<sub>12</sub>) had a much higher mortality on *M. alternatus* than on *S. populnea* (Fig. 3a;  $t$ -test:  $t_{38} = 10.874$ ,  $P < 0.001$ ). Moreover, the Ma colony (F<sub>12</sub>) had a lower proportion of male offspring on *M. alternatus* than the Sp colony (Fig. 3b;  $t$ -test:  $t_{38} = -2.640$ ,  $P < 0.05$ ). Similarly, the proportion of male offspring on *S. populnea* was significantly higher than on *M. alternatus* (Fig. 3b).



**Fig. 1** Comparison of fitness consequences of *Sclerodermus harmandi* from different culturing systems on different hosts: **a** fecundity (eggs per female), **b** pre-oviposition period (days), **c** oviposition period (days), **d** mean development rate of female offspring, **e** mortality (%), and **f** sex ratios (proportion of male).

## Discussion

The process of adaptation to a novel host may be determined by behavioral and physiological responses of parasitoids to that host (Henry et al. 2008). The present study showed that the adaptation

Abbreviations used: *Ma* larvae of *Monochamus alternatus*; *Sp* larvae of *Saperda populnea*; *Ma* colony parasitoids from Ma-reared colony; *Sp* colony parasitoids from Sp-reared colony (mean  $\pm$  SE,  $n = 20$  in each treatment)

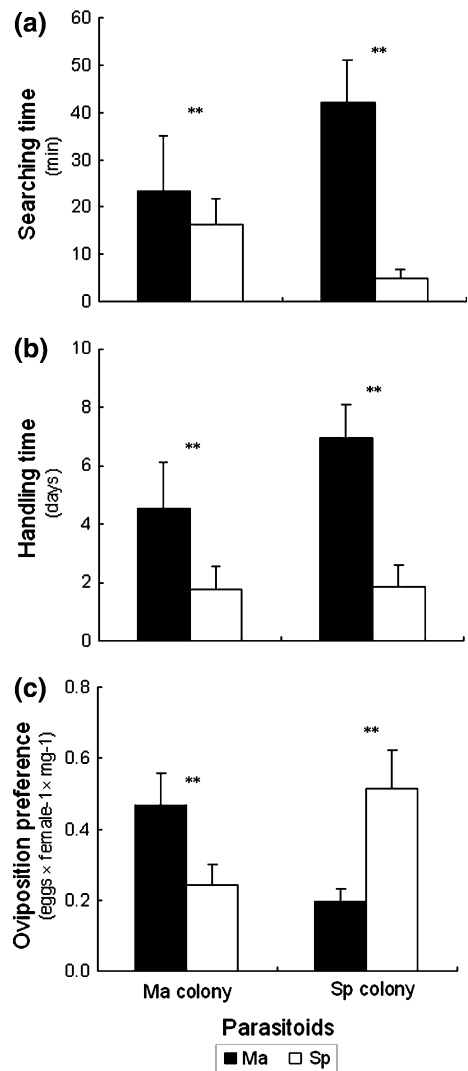
of a parasitoid *S. harmandi* to a new target host occurred faster than expected, in fewer than 12 generations (ca. 12–14 months). A positive relationship between fecundity and generation number was revealed during target host rearing over 12 successive generations. *S. harmandi* females of the 12th

**Table 2** Analysis of variance for fitness consequences of *Sclerodermus harmandi* from different culturing systems on different hosts (ANOVA,  $n = 25$  in each treatment)

Source	SS	df	F	P
Adult performance searching time (min)				
Colony	0.034	1	0.065	0.799
Host	129.073	1	244.054	<0.001
Colony $\times$ host	61.303	1	115.912	<0.001
Error	40.194	76		
Handling time (days)				
Colony	1.669	1	20.261	<0.001
Host	22.378	1	271.661	<0.001
Colony $\times$ host	1.202	1	14.595	<0.001
Error	6.260	76		
Oviposition preference (eggs $\times$ female <sup>-1</sup> $\times$ mg <sup>-1</sup> )				
Colony	0.001	1	0.080	0.778
Host	0.066	1	9.397	<0.005
Colony $\times$ host	1.725	1	244.136	<0.001
Error	0.537	76		
Offspring performance mortality (%)				
Colony	0.693	1	38.521	<0.001
Host	0.517	1	28.745	<0.001
Colony $\times$ host	0.782	1	43.427	<0.001
Error	1.368	76		
Sex ratio (% male)				
Colony	0.002	1	0.928	0.338
Host	0.039	1	24.059	<0.001
Colony $\times$ host	0.007	1	4.482	0.038
Error	0.125	76		

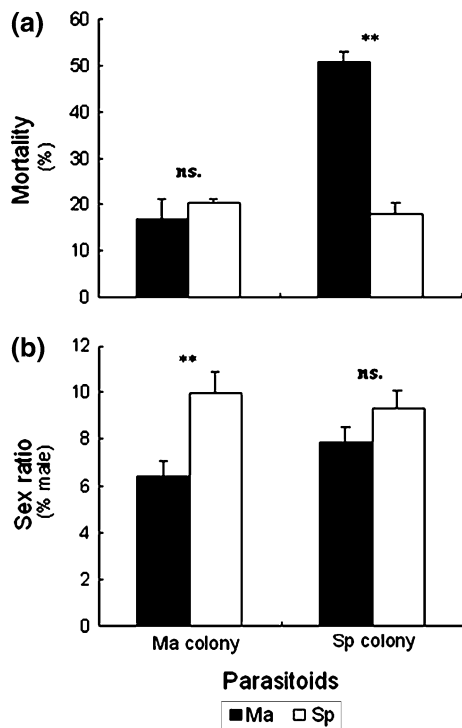
generation on the target host *M. alternatus* showed better performance, i.e., shorter time for searching and handling, higher oviposition preference, and, subsequently, lower offspring mortality and proportion of males on the host than those from *S. populnea* (the base stock). Moreover, females developed on the target host always had a lower proportion of male offspring on *M. alternatus* than *S. populnea* over multiple generations.

One of the costs of biological control relates to the production of needless males and the alterations of parasitic potential during the mass-rearing of parasitoids on substitute hosts. Surprisingly, we observed that the progeny sex ratio of *S. harmandi* was mainly determined by host species. In most gregarious parasitoids, the behavioral strategies under sex allocation are affected by host quality or host species



**Fig. 2** Searching time and handling time of  $F_{12}$  adult females from different culturing systems to different hosts: **a** searching time (min), **b** handling time (days), and **c** oviposition preference (eggs  $\times$  female<sup>-1</sup>  $\times$  mg<sup>-1</sup>). For abbreviations, see Fig. 1 (mean  $\pm$  SE,  $n = 25$  in each treatment,  $**P < 0.01$ )

(Bezemer and Mills 2003; Lentz and Kester 2008). The extent to which they successfully exploit a host for reproduction represents its fitness, with selection favoring those mechanisms that maximize fitness. *S. harmandi* females were able to produce broods with a female-biased sex ratio when there is a possibility that some of her offspring mate amongst themselves, and when the host quality varies, they will determine the sex of their own offspring by whether they fertilized the egg or not. This proximate



**Fig. 3** Comparison of offspring fitness consequences of  $F_{12}$  females from different culturing systems on different hosts: **a** mortality (%) and **b** sex ratio (proportion of males). For abbreviations, see Fig. 1 (mean + SE,  $n = 25$  in each treatment, \*\* $P < 0.01$ , ns.  $P > 0.05$ )

control of the sex ratio had allowed the evolution of locally adapted sex ratio (Godfray 2004).

Much of the current research has already utilized the host-size-dependent sex ratio manipulation procedure to successfully obtain more female-biased sex ratio in mass-reared cultures of parasitoids (Charnov et al. 1981; Ode and Heinz 2002). Practically, the ability to artificially induce more female-biased sex allocation in mass-reared cultures of parasitoids has widespread potential. This technique holds the greatest promise of success in solitary parasitoids of hosts that cease to develop after parasitism (idiobionts) (Waage 1982; Godfray 1994; King 1989). However, for gregarious parasitoids, their fitness was determined mainly by host species rather than a direct effect of host size (Godfray 1994). Our results showed that *S. harmandi* females had higher fecundity, stronger foraging potential, and lower proportions of male offspring when developed on high-quality host species than on low-quality host species. The female-biased sex ratio that varied with host quality was

available to regulate the sex ratio of *S. harmandi* in mass-rearing (Chambers 1977; Cohen et al. 1999).

Some insectaries also modify the sex ratio of *S. harmandi* through manipulating small groups of females exposed to more hosts (Chen and Cheng 2000). This mass-rearing method may reduce the probability of parasitoid inbreeding, but does not decrease the proportion of male offspring. In our analysis of interactions of generation/colony and host species, some solutions of monitoring mating behavior and sex ratio of *S. harmandi* to improve its mass-rearing may be presented, likely reducing the need for frequent releases. Regulating the optimal rates of hosts and parasitoids according to different host species is required to increase parasitoid fecundity. Moreover, monitoring parasitoid colonies on substitute hosts mated with those on target hosts may raise the reproductive ability of parasitoids and restore their parasitism to target hosts in the field. Last but not least, we can regulate host species or host sizes to reduce the proportion of male offspring in their mass-propagation of parasitoids. By presenting female *S. harmandi* groups of sequentially larger hosts to attack, more broods with female-biased sex ratios were generated progressively.

The success of inundative biological control of *M. alternatus* with *S. harmandi* depended on its efficient mass-rearing. Our experiments focused on how biological and behavioral adaptations of the parasitoid *S. harmandi* can be rapidly shaped to a target host. However, there are still some challenges to restore *S. harmandi*'s parasitism to target hosts in the field and improve its mass-rearing efficiency in the laboratory. Future work should pay more attention to investigating the learning potential of *S. harmandi* and its behavioral and physiological conditioning through the regulation of chemicals during the mass-rearing, as well as the artificial diet used during in vitro culture in order to improve its mass-rearing efficiency and parasitism in the field.

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