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Original Article

Host stage preference and suitability of *Allotropa suasaardi* Sarkar & Polaszek (Hymenoptera: Platygasteridae), a newly identified parasitoid of pink cassava mealybug, *Phenacoccus manihoti* (Homoptera: Pseudococcidae)

Md. Akhtaruzzaman Sarkar[1]*, Wiwat Suasa-ard[2], and Sopon Uraichuen[2]

[1] *Division of Entomology, Bangladesh Agricultural Research Institute, Joydebpur, Gazipur-1701, Bangladesh.*

[2] *Department of Entomology, Faculty of Agriculture, Kasetsart University, Kamphaeng Saen Campus, Kamphaeng Saen, Nakhon Pathom, 73140 Thailand.*

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Abstract

Allotropa suasaardi Sarkar & Polaszek (Hymenoptera: Platygasteridae) has been recently reported as a gregarious endoparasitoid of the pink cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Homoptera: Pseudococcidae) in Thailand. With the aim of improving mass production of this parasitoid, laboratory experiments were conducted comparing the parasitoid's preference on different host stages of mealybug, host suitability and its effect on parasitism, development, progeny fitness and sex ratio. All nymphal stages and adult of *P. manihoti* were parasitized by the parasitoid. However, host stage preference and suitability tests showed that the parasitoid had a significant preference for the older host stages. Percentage parasitization was higher in the third instar and early adult female stages compared with the first and second instar host. Mean developmental time for male parasitoids was shorter than for the females. Higher percentage emergence of parasitoid was observed from older mealybugs. Sex ratios of the offspring produced by the parasitoid were varied in different host stages and the ratio of female to male was higher in the older host stages. The implication of this host selection behavior for mass rearing of *A. suasaardi* and for evaluating it in a biological control program of the cassava mealybug are discussed.

Keywords: *Allotropa suasaardi* Sarkar & Polaszek, *Phenacoccus manihoti* Matile-Ferrero, host stage selection, host preference, host suitability

1. Introduction

The pink cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Homoptera: Pseudococcidae), is one of the most severe pests of the cassava (*Manihot esculenta* Crantz) in the world (Bellotti *et al.*, 1999). It is native to South America (Löhr *et al.*, 1990), but it has become naturalized throughout sub-Saharan Africa since its inadvertent introduction into the continent in the early 1970s (Neuenschwander, 2001). *P. manihoti* was not known to occur in Asia until 2008, when it was first detected in Thailand (Parsa, 2012). Its population hits its peak during the dry season (Hillocks *et al.*, 2001) and rainfall is thought to repress *P. manihoti* mainly by causing mechanical mortality (Le Rü and Iziquel, 1990). In recent times the parasitoid *Allotropa suasaardi* Sarkar & Polaszek (Hymenoptera: Platygasteridae) was described from a series of specimens reared from *P. manihoti*. The parasitoid was collected from a cassava field that was badly infested with mealybugs in the Kanchanaburi province (14° 0′ 15″ N, 99° 32′ 57″ E), Thailand′s third largest of 77 provinces. About 25 species of *Allotropa* Forster, 1856 have been described and they are known as primary endoparasitoids of various

* Corresponding author.
Email address: anuakhtar@yahoo.com

mealybugs (Masner and Huggert, 1989; Vlug, 1995; Buhl, 2002). Twenty one species are described from all major biogeographic regions of the world, with five species described from the Nearctic region (Muesebeck, 1979).

Host stage preference is important to the study of parasitoid life history, host-parasitoid interaction, population dynamics and community structures. Host stage often has a significant impact on the development, survival and reproduction of the foraging parasitoid. It is also a key ecological variable which may have an influence on a parasitoid's rate of attack, survival of its immature stages and the sex ratio of its offspring. The choice of host stage is an important determinant for progeny fitness in parasitoids (Hagvar and Hofsvang, 1991). Generally, parasitoid fitness is positively correlated with host size especially for females (Charnov, 1982; King, 1993).

Host stage selection pattern on parasitoid development may differ between idiobiont and koinobiont parasitoid's (Askew and Shaw, 1986). Idiobiont parasitoids kill or paralyze their hosts immediately after parasitism and do not allow the hosts to continue growth. Host stage selection is more critical for idiobiont parasitoids because they have to select the most profitable or suitable host stage for the development of their offspring (Godfray, 1994). A koinobiont parasitoid is able to parasitize a wider range of host stages or body sizes, although preference for larger hosts is often demonstrated. Small hosts are comparatively more acceptable to the koinobiont parasitoids than to the idiobiont parasitoids because these small hosts grow into larger individuals thus providing more resources for the development of the koinobiont parasitoid larvae. With this in mind the present study reported here investigated the host stage selection of *P. manihoti* i.e. the acceptance of different host stages on the host susceptibility to parasitization, the parasitoid preference and the most suitable host stage for offspring development, sex ratio, in addition to mass produce of this newly identified parasitoid for the successful implementation of biological control and IPM program.

2. Materials and Methods

All experimental studies and rearing were carried out in the laboratory of National Biological Control Research Center, Kasetsart University, Kamphaeng Saen Campus, Nakhon Pathom, Thailand during 2011-2012.

2.1 Rearing of *P. manihoti*

Mealybugs were collected from an infested cassava field in Kanchanaburi province, Thailand. After collection, the mealybugs were reared on ripe medium-sized Thai pumpkins *(Cucurbita moschata* Duchesne) fruits (approximately 20 cm in diameter) as an artificial host for the stock culture. The pumpkins were selected with ridges, furrows and small stalks which made the handling operation very easy. To prevent rotting, the pumpkins were treated with 0.1% benlate and 5% formaldehyde solutions and left 1 to 2 hours under shade to dry. The pumpkins were kept on stands and arrange in a cabinet comprising of five plywood shelves measuring 40× 100 cm and placed 35 cm apart, resulting in an overall height of 1.75 m. Each pumpkin was infested with 100 adult female mealybugs having well-formed ovisacs. Egg sacs and crawlers of different species of the mealybug were dusted individually on the upper surface for settling and development. Monthly infestations ensured a continuous supply of different nymphal instars. Adult females with ovisacs were available after 4-6 weeks. The cultures were maintained in the dark at 27±2°C.

2.2 Rearing of *A. suasaardi*

Pumpkins bearing 15 to 20 days old *P. manihoti* were offered to adult *A. suasaardi* for parasitization in 40 x 40 x 40 cm transparent plastic rearing cages, each having two openings, close up with black cloth. To ensure a continuous source of parasitoid, 100 adult females *A. suasaardi* were released on to newly mealybugs infested pumpkins every fifteen days. As adult parasitoids emerged from the parasitized mealybug, they were collected within 24 h of emergence and released into a plastic vial. Streaks of diluted honey were provided as food. To ensure mating and a full complement of eggs, the parasitoids were held in isolation for 48 h. As no hosts were provided during the holding period; the parasitoids were inexperienced when used in the experiments. The rearing environment was maintained at 27±2°C and 60±10% relative humidity (RH) under a 12: 12 light: dark photoperiod. Light was provided by a white fluorescence tube light (Lamptan, Fl 18W Ex-D Tri-phosphor), fitted in the shelf 30 cm above the cages and the light: darkness cycle was maintained using an electric timer switch. This procedure was continued during the experimentation period. Voucher specimens of these parasitoids have been deposited in the Natural History Museum of London.

2.3 Host stage susceptibility (No-choice experiments)

For the susceptibility of the parasitoid, *A. suasaardi*, the first, second, third instar nymphs and early adult females of the host were tested. Individuals of *P. manihoti* of the same age (1st, 2nd and 3rd instar nymphs and adult females within 24 h of molting) were maintained in the laboratory. Twenty mealybugs of the same instar were transferred onto a cassava leaf and placed in groups in separate Petri dishes (6 cm in diameter and 1.5 cm in depth). The following day, a single mated female of *A. suasaardi* was introduced individually into the Petri dish containing a mealybug-infested leaf. After 24 h of exposure, parasitized mealybugs were transferred to jars. The number of hosts parasitized and the percent parasitization were recorded for the parasitoids from each respective host stages. Twenty groups were exposed to different individual *A. suasaardi* females in this manner.

2.4 Host stage preference (Choice experiments)

Mixed population of 1st, 2nd and 3rd instar nymphs and early adult females of *P. manihoti* in equal proportions (five mealybugs of each stage) were transferred to each selected cassava leaf and kept in a Petri dish described as above; a single mated female parasitoid was introduced into each experimental arena for 24 h. Twenty groups were exposed to different individual *A. suasaardi* females in this manner.

2.5 Host stage suitability

Thirty mealybugs of the same stages (1st, 2nd and 3rd instar nymphs and early adult females) were transferred onto cassava leaf and placed in a transparent plastic jar (6 cm long and 3.5 cm in diameter), the top covered with fine net. Three adult female parasitoids were introduced for a period of 24 h. The parasitized mealybugs of each instar were then placed separately onto a small plastic dish (4 cm in diameter and 1.5 cm in depth) until adult emergence. The mealybugs were observed on a daily basis to record parasitoid emergence. The emergence data and sex of each parasitoid were recorded. The sex ratio and the developmental period of the parasitoids emerging from different stages were determined.

2.6 Statistical analysis

Data of host susceptibility, host preference, host suitability and developmental period were subjected to a one-way ANOVA. Prior to analyze, percentage parasitization and emergence data were transformed by square-root and arc sine where needed. Numbers are given as mean ± standard deviation.

3. Results

3.1 Host stage susceptibility (No-choice experiments)

All four stages of *P. manihoti* were parasitized by the parasitoid *A. suasaardi*. It revealed that adults were the most parasitized stage and first instar was the least. The rate of parasitization was similar. The mean number of host stages parasitized and parasitization rate was highest (11.42±1.64; 57.11% respectively) in adult female which was highly significant ($P<0.01$) than that of the first and second instar stages. Third instar received 10.32±1.57 mean number hosts parasitized and parasitization rate 51.58%; which were statistically similar with adult stage (Table 1). The first instar mealybug obtained the least number of host parasitized (2.16±1.12) and also the lowest parasitization rate (10.79%). Mean number of host stages parasitized and parasitization rate was increased significantly with the increase of host size.

3.2 Host stage preference (Choice experiments)

Female *A. suasaardi* parasitized all developmental stages in the choice experiment. The results of mean number of host stage parasitized and parasitization rate in the choice test demonstrated a comparatively similar trend to the no-choice but was lower in all host stages. Significantly ($P<0.01$) higher number parasitized stages (2.53 ± 0.77) and parasitization rate (50.53%) was obtained from adult female which was followed by the third instar (2.26±0.43, 45.26% respectively). The least parasitized first stage achieved 0.11±0.31 parasitized stages and 2.11% parasitization rate respectively (Table 1). In the choice tests, *A. suasaardi* showed clear preference for third instar and adult stage mealybugs.

3.3 Host stage suitability

Successful development and emergence of parasitoid progeny were observed from all the stages of *P. manihoti*. The percentage emergence was significantly ($P<0.01$) higher in the adult female mealybugs than in the earlier host stages (Table 2). The highest emergence rate occurred in the adult stage (63.94%) followed by the third instar (54.59%) compared to second (19.12%) and first instar (12.28%) (Table 2).

Table 1. Host stage acceptance and preference by *A. suasaardi* in no-choice and choice experiments in different stages of *P. manihoti*. For each host stage, twenty individuals were exposed to one female parasitoid for 24 h.

Host stage	Age (days)	No-choice experiment		Choice experiment	
		Mean (±SD) no. hosts parasitized	Parasitization (%)	Mean (±SD) no. hosts parasitized	Parasitization (%)
First instar	5	2.16 ± 1.12 c	10.79 c	0.11 ± 0.31 b	2.11 b
Second instar	10	4.37 ± 1.38 b	21.84 c	0.42 ± 0.50 b	8.42 b
Third instar	15	10.32 ± 1.57 a	51.58 b	2.26 ± 0.43 a	45.26 a
Adult female	20	11.42 ± 1.64 a	57.11 a	2.53 ± 0.77 a	50.53 a
LSD value		1.238	2.958	0.483	5.026

Values are means ± SD, N = 20. Different letters within each column indicate that the values differ with high statistical significance ($P<0.01$; LSD test).

Table 2. Mean emergence (%) and developmental time of *A. suasaardi* from different stages of *P. manihoti*.

Host stage	Age (days)	% Emergence	Mean developmental time (days) ±SD	
			Female	Male
First instar	5	12.28 c	26.37 ± 1.11 a	23.84 ± 1.30 a
Second instar	10	19.12 b	25.74 ± 1.17 a	22.63 ± 1.49 b
Third instar	15	54.59 a	23.47 ± 1.12 b	20.95 ± 1.13 c
Adult female	20	63.94 a	22.42 ± 1.54 b	20.06 ± 1.07 c
LSD value		9.687	1.068	1.082

Values are means ± SD, N = 20. Different letters within each column indicate that the values differ with high statistical significance (P<0.01; LSD test).

3.4 Developmental time

A. suasaardi successfully completed development in all host stages of the mealybug. Highly significant difference (P<0.01) was observed in the developmental duration of male and female individual in all four stages. It was revealed that in both sexes, developmental time decreased with the age of host and showed a negative linear manner with different host stages at parasitization. However, females in general took longer to develop than males. The female parasitoids that emerged from the first instar host took about 26 days whereas, the male took 24 days and developed from the adult stage took about 22 days and 20 days, respectively (Table 2).

3.5 Sex ratio

The host stage at which parasitization occurred also had significant influence on the progeny sex ratio of *A. suasaardi*. The progeny sex ratio of *A. suasaardi* attacking the youngest stage produced male biased offspring but the oldest stage produced female biased offspring. The proportion of males was reduced when the hosts were attacked in the second and third instar mealybugs (Figure 1). It was observed from the figures that the proportions of male parasitoids decreased with increasing host age and showed negative linearity.

4. Discussion

4.1 Host stage susceptibility and preference

A. suasaardi parasitized all developmental stages of *P. manihoti* but showed a preference for the adult stage over other nymphal stages offered simultaneously. Although the susceptibility and preference of the parasitoid were considered independently, the trend of the number of host stage parasitized and parasitization rates were similar in both experiments. In the no choice experiment the younger stages attained a lower parasitization rate; this might be owing to their tiny size as well as the fast movement of the crawler with consequently less frequent encounters with the parasitoid. But in the following older stage the rate of parasitization gradually increased; this may be due to the bigger host size, less escape and less defensive behavior which enables it to be sought and found by the parasitoid more easily. Islam and Copland (1997) also observed a lower parasitization rate by the parasitoid *Anagyrus pseudococci* (Girault) in second instar of the citrus mealybug, *Planococcus citri* (Risso) due to their size and that the feeding sites were less encountered by the parasitoid. Jervis and Kidd (1986) observed that hosts that are fed on are usually not suitable for egg deposition due to the depletion of resources and death of the hosts. Luck *et al.* (1982) and Rosenheim and Rosen (1991) observed *Aphytis* species (Hymenoptera: Aphenilidae) and suggested that parasitoids preferentially host feed on small hosts and oviposit on larger hosts. *Anagyrus mangicola* Noyes host fed on crawlers and second-instar nymphs of *Rastrococcus invadens* William and did not oviposit in these individuals (Bokonon-Ganta *et al.*, 1995). We did not observe host feeding by *A. suasaardi* in this study. In the choice tests, *A. suasaardi* significantly preferred the adult stages over the other stages. Even though crawlers were encountered and

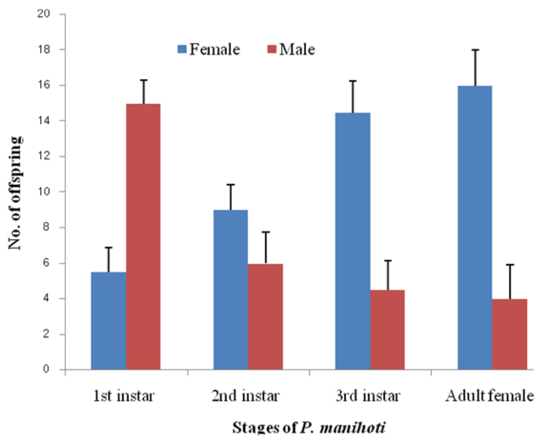

Figure 1. Sex ratio of *A. suasaardi* in response to different stages of *P. manihoti*. Vertical bar represents mean ±SD values.

examined, they were parasitized at a lower rate. *Allotropa utilis* Muesebeck, a solitary parasitoid, is reported to parasitize younger nymphs of its host (Murakami, 1963). Clancy (1944) found that *Allotropa burrelli* Muesebeck, a gregarious parasitoid, parasitized mealybugs in the third instar or in the early adult stage and produced the greatest number parasitoids. The result of the present study is in agreement with that findings. It was reported that *A. mangicola* and *Anagyrus kamali* Moursi attacked all developmental stages of their respective hosts but preferred the larger and more advanced host stages over the smaller and younger stages (Bokonon-Ganta *et al.*, 1995; Sagarra and Vincent, 1999). Nechols and Kikuchi (1985) observed that *Anagyrus indicus* Shafee, Alam and Agarwal prominently preferred older host stages in the spherical mealybug, *Nipaecoccus viridis* (Newstead). In the no-choice tests *A. indicus* parasitized hosts at all developmental stages. However, when given a choice of host stages *A. indicus* completely ignored the crawlers and second-instar nymphs and had a strong preference for adult mealybugs and to a lesser extent the third-instar nymphs of the *N. viridis*. DeJong and van Alphen (1989) observed in another encyrtid, *Leptomastix dactylopii* How. that it preferred the older stages of *P. citri*.

4.2 Host stage suitability

A. suasaardi developed successfully from all the developmental stages of *P. manihoti*. The results revealed that early adult females (20 days old) were the most suitable host stage for the development and survival of *A. suasaardi*. The emergence percentage was relatively higher in third instar compared to first and second instar. The observations of this study evidently indicated that the younger stages (5 and 10 days old) were less suitable for the development of *A. suasaardi* where a lower emergence percentage was found in early stages. Jervis and Copland (1996) reported that the parasitoid accessed a larger food supply and increased the fitness of its progeny when they chose a larger host. Considering the above observation, the possible reason for the lower emergence percentage obtained in the younger stages in this study was an inadequate food supply; which restrained the parasitoid development. Successful oviposition is also one of the major factors to influence emergence. So far, in 5- and 10- day- old instars, the attempt of successful oviposition by the parasitoid may be lower, with a consequence that decreased offspring production prevails. Mani and Krishnamoorthy (1989) found the maximum number of parasitoid emergence when third instar of *Maconillicoccus hirsutus* (Green) nymphs were offered to *Allotropa japonica* sp. n. for parasitization, whereas 20-days- old *P. manihoti* adults provided the highest emergence followed by the third instar in the present study. Cadee and van Alphen (1997) found that hosts attacked by koinobiont parasitoids continue to grow to a later stage and some are even able to reproduce before death. Harvey *et al.* (1994) reported that koinobiont parasitoids may suspend feeding and development in younger hosts until the hosts achieved an appropriate stage, thus with sufficient resources, to support the resumed development of the parasitoid larvae. Smilowitz and Iwanstch (1975) observed that hormonal cues from the host stimulate the development and destructive feeding of the first instar solitary koinobiont parasitoid *Hyposoter exiguae* (Viereck) (Hymenoptera: Ichneumonidae), which was suspended in young caterpillars.

4.3 Developmental time

The older the stage of *P. manihoti* that was attacked, the faster *A. suasaardi* would develop. Larger hosts provide more resources, making size a reliable indicator of the amount of resources available for parasitoid development. The developmental times from third instar and early adult females were identical for both sexes of the parasitoid. Nevertheless, male parasitoids emerged much sooner than females from hosts parasitized in the first instar and second nymphal stage. The developmental time of the parasitoid was later in the first and second instars than third and early adult. Löhr *et al.* (1988) found a similar trend in the developmental time of the parasitoid *Epidinocarsis lopezi* (DeSantis) in the early stage host of cassava mealybug, *P. manihoti*. This might be due to insufficient food sources in the younger stages of the host resulting in a lower nutrient supply to the parasitoid during the parasitization. Different developmental rates of *Diaeretiella rapae* (M'Intosh) in different instars of its host were observed by Liu (1989) and these were believed to be due to differences in host body size and nutritional quality. However, developmental time of *A. suasaardi* is most favorable in both the third instar and early adult hosts; males and females both developed fastest in early adult host. The developmental duration of this parasitoid is similar to that of *A. bureli* (Clancy, 1944) and *A. japonica* (Mani and Krishnamoorthy, 1989).

4.4 Sex ratio

Host stage is one of the key determining factors to manipulate the sex ratio; the results of the present study also reflected this. The sex ratio of *A. suasaardi* emerging from hosts that were parasitized as first instars was strongly male biased, while the apparently preferred later stages yielded significantly more females than males. Third instar and adult females produced more female parasitoids, while first instar produced more males. This may explain the preference for the third instar and adult as well as the female-biased sex ratio, as age is usually positively correlated with higher fitness, especially in females. King (1993) observed female-biased sex ratios in older hosts in hymenopterans parasitoids. Many species of parasitoid wasps have a tendency to lay male and female eggs in different types of hosts: typically, males are laid in relatively small hosts, and females in relatively large hosts. Charnov et al. (1981) argued that females gain more than males do from developing in larger hosts. A decrease in the male ratio with an increase of host size has been demonstrated in different mealybug parasitoids by Nechols and Kikuchi (1985), Kraaijeveld and van Alphen (1986), Löhr *et al.* (1988), Mani and Krisnamoorthy (1989); and the present study is in agreement with that reports. Sequeira and Mackauer (1993) reported male-biased populations of *Aphidius ervi* (Haliday) emerging from small pea aphids. *A. ervi* deposits fertilized eggs in large hosts and unfertilized eggs in small ones (He and Wang, 2006). Bertschy *et al.* (2000) found the proportion of female emergence was the greatest in third instar mealybugs followed by the adult stage in *Aenasius vexans* Kerrich against the cassava mealybug, *P. manihoti*. Loehr (1991) observed female biased sex ratio (2:1) of *Allotropa* sp. parasitized *P. manihoti*. Mani and Krishnamoorthy (1989) found that *A. japonica* produced 60.16% male in first instar *M. hirsutus* (Green) but all the later stages of the mealybug produced predominantly female parasitoids. A similar trend was observed in this study.

5. Implications for Biological Control Program

Based on the results of this study, in order to achieve the goal of producing high quality *A. suasaardi*, faster development, female biased sex ratio as well as higher survival rate, the mass rearing system has to be designed with a high proportion of the mealybug population consisting of third-instar nymphs and early adult females.

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