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Influence of parasitoid-host density on the behaviour ecology of *Goniozus nephantidis* (Muesebeck) (Hymenoptera: Bethylidae), a parasitoid of *Opisina arenosella* Walker

T. VENKATESAN, K. SRINIVASA MURTHY, R. J. RABINDRA and T.V. BASKARAN

National Bureau of Agriculturally Important Insects, Post Bag No. 2491, H. A. Farm Post, Hebbal, Bangalore 560024, Karnataka, India.

E-mail: chrysopa1@yahoo.com

ABSTRACT: Since *Goniozus nephantidis* (Muesebeck) is found to have strong parental care for its progeny, the influence of different densities of *G. nephantidis* and its host, *Corcyra cephalonica* (Stainton) on the behaviour ecology of the parasitoid was studied. Interaction between different densities of the host and parasitoid revealed that a ratio of 1: 1 was significantly superior to all other ratios resulting in maximum parasitism (9.0 larvae / female), fecundity (93.2 / female) and number of progenies (75.2 / female). Exposing more than one *C. cephalonica* larva did not significantly increase the parasitizing efficiency, fecundity and progeny produced. Conversely, exposing a single *C. cephalonica* larva to several female parasitoids adversely affected the biological attributes of the parasitoid. Increasing the densities of either host insects or parasitoids had an inverse relationship with oviposition behaviour, parasitism efficiency and progeny production of the parasitoid establishing the important and significant role played by host–parasitoid density.

KEY WORDS: *Corcyra cephalonica,* density, *Goniozus nephantidis, Opisina arenosella,* parasitizing behaviour, parental care

INTRODUCTION

Goniozus nephantidis (Muesebeck) (Hymenoptera: Bethylidae) is the dominant parasitoid responsible for the reduction of the coconut black-headed caterpillar *Opisina arenosella* Walker. The pest is an endemic, frequently outbreaking pest of coconut in India and Sri Lanka and occurs also in Myanmar and Bangladesh (Dharmaraju, 1963; Cock and Perera, 1987; Venkatesan *et al*., 2006). *G. nephantidis* parasitizes 3^{rd} to 7^{th} instar larvae of *O. arenosella*. The natural parasitism levels of *G. nephantidis* on *O. arenosella* vary from 3.7 to 57.6 in India (Kapadia, 1987).

The female of *G. nephantidis* attacks and paralyses the lepidopteran larvae by envenomizing them. Then the parasitoid lays a clutch of 10 to 18 eggs (Cock and Perera, 1987; Hardy, 1995; Venkatesan *et al*., 2003) approximately a day after paralyzing the host (Goubault *et al*., 2007a). The female parasitoid remains with their broods following oviposition until the offspring reach an advanced stage of development (Antony and Kurian, 1960; Cock and Perera, 1987; Remadevi *et al*., 1981; Hardy and Blackburn, 1991). However, the parasitoid is physiologically capable of laying more clutches at more frequent intervals than this behaviour allows (Hardy and Blackburn, 1991). Females with paralyzed but unparasitized hosts defend this resource against any intruder females that encounter and contest it. Contest involves aggressive postures, rapid chases, and violent fights in which contestants attempt to bite and sting each other, while rolling around on the substrate like a ball. The first female to break away from a fight is the loser. Loser females almost always survive the interaction, but usually stay distant from both the winner and the host and it is the winner that eventually lays eggs on the host (Hardy, 2006).

Corcyra cephalonica (Stainton) (Lepidoptera: Pyralidae) is used as an alternative host for the mass production of *G. nephantidis* in the laboratory in India. Parental care or brood guarding is a common behavioural phenomenon encountered in *G. nephantidis* during laboratory production either on target pest or on alternate host and this behaviour may affect the efficiency of the parasitoid against the target pest during field release programmes. Keeping this in view, the objectives of the present study were to determine the influence of different densities of *C. cephalonica* larva and a female of *G. nephantidis vis–a–vis* when reciprocated (different densities of parasitoid females and single host larva) on parasitism, fecundity, longevity and progeny production.

MATERIALS AND METHODS

Insect Rearing

Stock culture

The culture of *G. nephantidis* was started with field–collected individuals from *O. arenosella*–infested orchards in Bangalore (India) during 2004 and successfully continued on the late instar larvae (5–7th) of *C. cephalonica*.

Bioassay procedures

The experiments were conducted at 26 ± 1ºC, 65 ± 5% RH and a 14L: 10D light: dark regime. After emergence, males and females of *G. nephantidis* were released in a clear plastic container (1 litre capacity) and left to mate for 24h (Gordh, 1976). After this, males were discarded using a fine brush. Diluted honey (50 %) and a cotton swab moistened with water were provided as adult food (Venkatesan *et al.*, 2004). After a pre–oviposition period of 6 days, the females of *G. nephantidis* were separated and kept in glass tubes (5.7 x 2.5 cm) and provided with diluted honey (50 %) streaked in polythene strips.

Corcyra cephalonica was used as a host insect for studying the influence of different densities of parasitoid and the host on the behaviour ecology of the parasitoid. *C. cephalonica* larvae were reared on broken sorghum grain based media (Jalali *et al*., 2003). Mature *C. cephalonica* larvae (5th–7th instar) were picked up from the galleries and released individually into each vial. The following treatments were imposed for the study on the influence of different densities of *C. cephalonica* and single female of *G. nephantidis* on parasitism (total number of larvae parasitized per parasitoid; fecundity, longevity and progeny production of the parasitoid [1 H (Host): 1 W (Wasp), 2: 1, 3: 1, 4: 1, 5: 1 and 6: 1]. In ratios 2: 1 to 6: 1 (H: W), parasitized larvae were removed and replaced with fresh larvae till the parasitoid died. Similarly, the influence of different densities of *G. nephantidis* females and single *C. cephalonica* on the above biological parameters was studied with the treatments [1 W: 1 H, 2: 1, 3: 1, 4: 1, 5: 1 and 6: 1] and the observations were recorded till the expiry of last female.

In each glass vial, diluted honey (50%) solution was provided as adult food as mentioned earlier after every 3 days till the female's death. Parasitized larvae having eggs of *G. nephantidis* were gently removed and kept in a transparent plastic box (6.0 x 6.0 cm).

Data Analysis

The study consisted of five treatments and was replicated five times. The data were subjected to one-way analysis of variance (ANOVA) and the means were separated by LSD test, whenever ANOVA was significant. The relationships between host-parasitoid density and parasitization, fecundity, longevity and progeny produced were evaluated by regression analysis.

RESULTS AND DISCUSSION

Influence of different host densities on parasitism, reproductive performance, longevity and progeny production of *G. nephantidis*

Goniozus nephantidis successfully parasitized at least one larva when exposed to more than one larvae. Developmental duration of *G. nephantidis* was 12.0 days. The number of larvae parasitized at different densities of *C. cephalonica* larvae and single *G. nephantidis* female varied from 3.4 to 9.0 and there was significant difference among different densities (ANOVA, $F = 7.99$; d. f. = 4, 5; $P < 0.05$). Maximum (9.0/female) and minimum number (3.4/female) of larvae parasitized was recorded in 1: 1 (*C. cephalonica* larvae: *G. nephantidis* female) and 4: 1, respectively. We discuss our results in terms of parental care, parasitizing and fighting behaviour of *G. nephantidis* females. Our study revealed that 1: 1 ratio was the best in terms of parasitism and progeny production among different ratios of exposure. Here paralyzed larvae along with eggs of *G. nephantidis* were considered as parasitized larvae. When exposed to more than one *C. cephalonica* larvae, the number of parasitized larvae by a single female was reduced. This is due to the fact that the female was found stinging and paralyzing the larvae rather than laying eggs on second, third, fourth, fifth and sixth larvae that were exposed subsequently. Pillai and Nair (1985) studied the mating and host paralyzing behaviour of *G. nephantidis*. Luft (1996) reported that females of *G. nigrifemur* (Ashmead) that responded to hosts exhibited behaviour patterns that were divided into three categories, *i.e.*, attack, host preparation and oviposition. Similarly, it was observed that *G. nephantidis* exhibited three categories of behaviour when a single female was exposed to single *C. cephalonica* larva. Perfect parental care was observed in female *G. nephantidis* wherein the parasitoid guards its eggs till they reach cocoon stage. The adult females were observed to feed on the haemolymph of the host larvae after making punctures and before paralyzing the larvae. Parental care in gregarious external parasitoids is more evident in the Chrysidoidea, particularly in several genera of Bethylidae (Griffiths and Godfray, 1988). Parental care especially in gregarious parasitoids like *G. nephantidis* could be advantageous as the egg, larvae and pupae of the parasitoid are always under risk for their susceptibility to hyperparasitoids or other natural enemies (Doutt, 1973). Female hymenopteran parasitoids provide their eggs with sufficient food resources for their development to adulthood. Females of some species increase their investment in each brood by remaining with the clutch until the offspring reach an advanced stage of development (Hardy and Blackburn, 1991). Recently, Goubault *et al*. (2007a) reported that *G. nephantidis* female paralyzes the host caterpillar and lays eggs onto it approximately one day later and then remains with the offspring during development until pupation. Parental care is always effective against conspecific intruders, which never superparasitize when the mother is present and unguarded eggs are always killed (Hardy and Blackburn, 1991).

When *C. cephalonica* larva was exposed to *G. nephantidis* alone, the parasitoid envenomized and paralyzed the larva within 3–5 h after release. Then, we observed that the parasitoid started biting, malaxating and making the larvae ready before laying a clutch of eggs. Such behaviour was observed in *G. nigrifemur* (Luft, 1996), *G. japonicus* (Ashmead) (Kishitani, 1961) and *G. gallicola* (Fouts) (Gordh, 1976). Parasitism by *G. nephantidis* led to shriveling and death of the host larvae and the matured parasitoids spun white or pale white cocoons adjacent to the host remains within 24 h of larval developmental period. The number of larvae parasitized in different host–parasitoid densities ranged from 6.0 to 10.2. Venkatesan *et al*. (2003) studied the parasitization efficiency of *G. nephantidis* in *O. arenosella, C. cephalonica* and *Galleria mellonella* (Linnaeus) which ranged from 6.5 to 9.4 per female. Generally, oviposition began within 24 h after paralysis and was completed within 48 h on a single host.

In general, the parasitoid was found to lay eggs on all parts of the body except head and abdominal end. Maximum fecundity was recorded at 1: 1 followed by 3: 1 and 2: 1, which were on par with each other and significantly higher than that of 4: 1, 5: 1 and 6: 1 (ANOVA, F = 5.93; d. f. = 4, 5; $P < 0.05$). The number of eggs laid per larva varied from 8-16. The adult females obtained from different densities had a longevity of 31.8 to 58.4 days and the maximum was observed at 1:1 density and there was no significant difference among the different densities (Table 1). The highest number of progeny (75.2 / female) was obtained at 1: 1, which was on par with 2: 1 (53.6) and 3: 1 (67.2) and the numbers were significantly higher than that of 4: 1 (28.4), 5: 1 (42.0) and 6: 1 (23.2) (ANOVA, F = 5.77; d. f. = 4, 5; $P < 0.05$) (Table 1). The proportion of females produced at different host densities ranged from 0.94 to 0.98 and were on par with each other.

Increase in the density of host insects produced a decrease in the number of larvae parasitized (Fig. 1) (F = 1.76; d. f. = 1,4, $P < 0.05$; $r^2 = 0.306$), fecundity and the mean number of progeny produced. Regression analysis indicated that the relationships between host density and the fecundity of the parasitoid (Fig. 2) (F = 20.51; d. f. = 1,4, $P < 0.05$; $r^2 = 0.837$) (Fig. 2) and also progeny produced (F = 10.87; d. f. =1, 4, $P < 0.05$; $r^2 = 0.731$) (Fig. 3) were significant. Mean fecundity was not affected at 1: 1 to 3: 1. However, fecundity was drastically reduced when four to six larvae were exposed. Increased availability of larvae did not contribute to significant increase in parasitization, fecundity and number of adults produced, suggesting the inherent capacity of the parasitoid and its behaviour to select, oviposit and develop on a particular larva, when more number of larvae were offered. Availability of more

Table 1. Influence of different host densities on parasitism, reproductive performance and longevity of *G. nephantidis*

Ratio (*Goniozus: Corcyra*)	Larvae parasitized (nos.)	Fecundity	Longevity (days)	Progeny produced (nos.)
1: 1	9.0[a]	93.2[a]	58.4	75.2[a]
1: 2	5.2[b]	75.0[a]	55.4	53.6[a]
1: 3	3.8[b]	81.2[a]	52.6	67.2[a]
1: 4	3.4[b]	43.4[b]	31.8	28.4[b]
1: 5	4.8[b]	54.6[b]	44.0	42.0[b]
1: 6	5.2[b]	31.6[b]	35.8	23.2[b]
SEM	0.7038	9.768	7.22 NS	8.683

Each mean represents five replications; means followed by the same letter are not significantly different at the 5 % level by DUNCAN's LSD test; NS Non–significant hosts for parasitization at a given point of time provides an option for the parasitoid to select and attack leading to a low preference for others. Host preparation and brood guard behaviour may offset the biological attributes on other larvae. Thus, females which remain with the clutch have a reduced reproductive potential which has some fitness cost (Tellamy and Denno, 1986). Such benefits may include protection of offspring against abiotic (Ichikawa, 1988) or biotic factors (Morse, 1988).

The sex ratio in mated *G. nephantidis* was always female-biased irrespective of the number of *C. cephalonica* larvae exposed. Parthenogenetic reproduction was observed in *G. nephantidis* by Antony and Kurian (1960). Per cent female produced at different densities was not affected. Female–biased sex ratio has been reported in other *Goniozus* spp. (Luft, 1996; Green *et al*., 1982; Hamilton, 1967). Population dynamic theory suggests that increasing the production of female offspring per host attacked will lead to greater host suppression (Heimpel, 2000; Murdoch and Briggs, 1996).

The maximum number of larvae (10.2 / female) was parasitized at 3: 1, which was statistically on par with 2: 1 (9.0 / female) and 1: 1. The number of parasitized larvae at these densities was higher than those at 4: 1, 5: 1 and 6: 1 densities (ANOVA, F = 4.20; d. f. = 4, 5; $P < 0.05$). The maximum fecundity (90.2 / female) was recorded at 1: 1, significantly superior to all other densities (2 – 6: 1) (ANOVA, F = 6.81; d. f. = 4, 5; $P < 0.05$), which resulted in rapid decrease in fecundity (21.2 – 39.2). The longevity of *G. nephantidis* females in different densities ranged from 16.0 to 49.8 days. Females at 1: 1 lived for 49.8 days and were significantly superior to all other densities (16.0 -

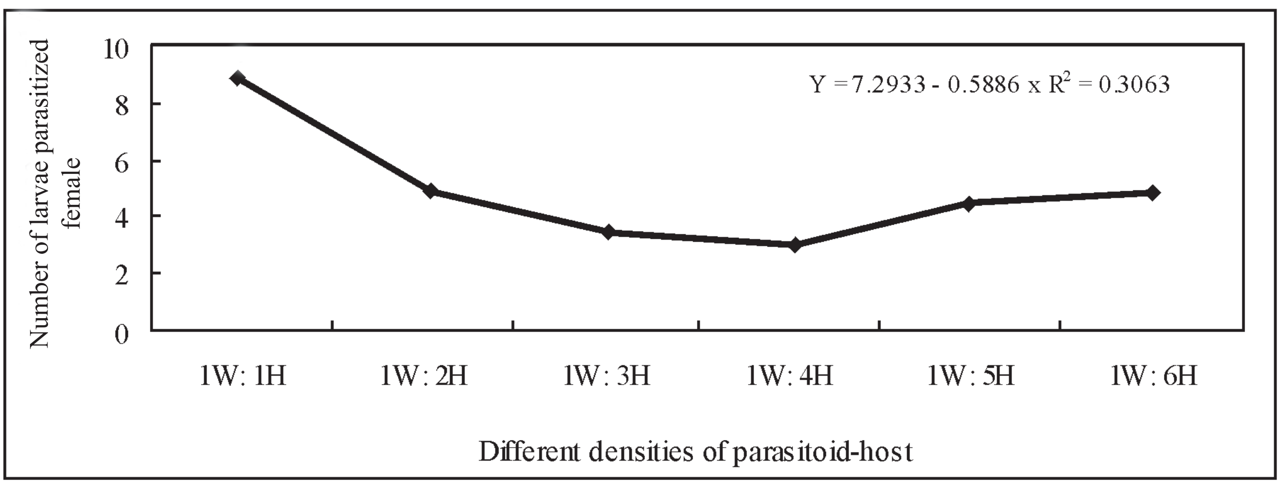

Fig. 1. Relationship between number of larvae parasitized per female parasitoid and host-parasitoid density

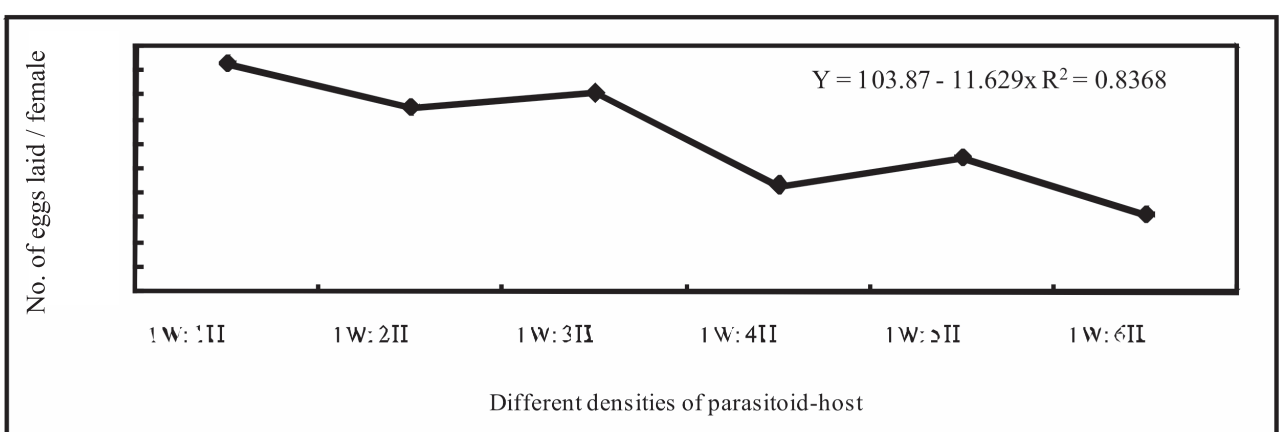

Fig. 2. Relationship between fecundity per parasitoid and host-parasitoid density

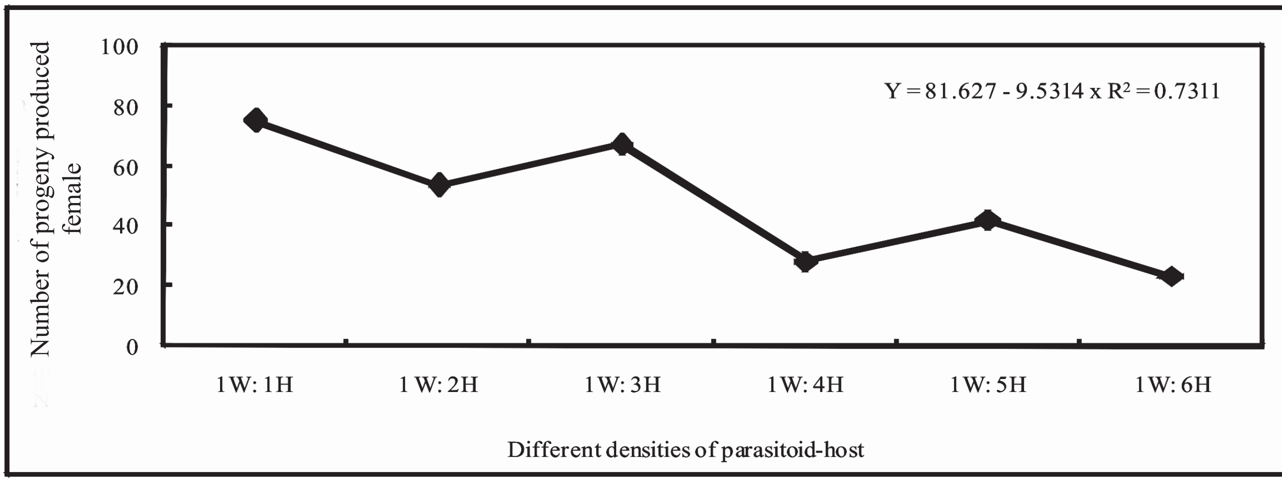

Fig. 3. Relationship between progeny produced by female parasitoid and host-parasitoid density Influence of different parasitoid densities on parasitism, reproductive performance, longevity and progeny production of *G. nephantidis*

21.2) (ANOVA, F = 7.06; d. f. = 4, 5; P < 0.05) (Table 2). The number of progenies at different densities ranged from 17.0 to 70.2 and the maximum was recorded at 1: 1, which was significantly higher than that at all other densities (17 – 33.4) (ANOVA, F = 5.37; d. f. = 4, 5; P < 0.05). Females produced in different densities ranged from 0.93 to 0.97 and there was no significant difference among various densities (P = 0.05) (Table 2) (Plate 1).

Increase in the density of parasitoids produced a decrease in the number of larvae parasitized (Fig. 4), decrease in the fecundity (Fig. 5) (F = 3.349; d. f. = 1, 4; P < 0.05; r^2 = 0.456), longevity (Fig. 6) (F = 0.426; d. f. = 1, 4; P < 0.05; r^2 = 0.426) and mean number of progeny produced by *G. nephantidis* (Fig. 7). Regression analysis indicated that the relationships between parasitoid density and the number of larvae parasitized (F = 0.561; d. f. = 1, 4; P < 0.05; r^2 = 0.561) and progeny produced (F = 5.192; d. f. = 1, 4, P < 0.05; r^2 = 0.565) were significant.

The fecundity, longevity and number of progeny obtained per larva were reduced with an increase of parasitoid numbers suggesting competition among themselves for oviposition, nourishment and development. When single *C. cephalonica* larva was exposed to more than one *G. nephantidis* female, altered behaviour was observed. The female parasitoids were fighting with each other for stinging and paralyzing the larva. The more robust female bigger in size and probably stronger than others,

Table 2. Influence of different *G. nephantidis* females on parasitism, reproductive performance and longevity of *G. nephantidis*

Ratio (*Corcyra: Goniozus*)	Larvae parasitized (nos.)	Fecundity	Longevity (days)	Progeny produced (nos.)
1: 1	9.0[a]	90.2[a]	49.8[a]	70.2[a]
1: 2	9.0[a]	39.2[b]	21.2[b]	33.4[b]
1: 3	10.2[a]	26.2[b]	16.0[b]	22.0[b]
1: 4	6.2[b]	21.2[b]	20.1[b]	17.0[b]
1: 5	7.4[b]	29.2[b]	21.1[b]	22.6[b]
1: 6	6.0[b]	33.0[b]	18.3[b]	21.8[b]
SEM	0.8287	9.739	4.740	8.579

Each mean represents five replications; means followed by the same letter are not significantly different at the 5 % level by DUNCAN's LSD test always dominated and was more successful in courting the larva. This phenomenon of large females being more successful in the host–ownership contests has been reported (Peterson and Hardy, 1996). When new intruder encounters guard hosts, brief aggressive owner-intruder contests usually result in the loser being driven from the vicinity of the host (Peterson and Hardy, 1996; Stokkeb & Hardy, 2000). Further, Stokkeb & Hardy (2000) attributed that wasps with higher egg loads were better able to exploit the host resource via oviposition and this gave a higher value to them than wasps with lower egg loads. Sometimes the adult female parasitoids were found killed while paralyzing the host larvae due to competition. This is in accordance with Perez–Lachaud *et al*. (2002) and Batchelor *et al*. (2006) who found that direct inter-specific contests frequently result in the paralysis and death of the defeated female. Goertzen and Doutt (1975) observed similar behaviour in other bethylids and van Alphen and Visser (1990) observed it in other parasitic families. Competitive fighting behaviour between *G. nephantidis* and *Bracon brevicornis* (Wesmael) was reported by Venkatesan *et al*. (2009). Fighting behaviour in other bethylids was reported by Doutt (1973), Batchelor *et al.* (2005, 2006), Humphries *et al.* (2006) and Goubault *et al*. (2006, 2007). Goubault *et al*. (2006) found that a volatile chemical (a spiroacetal, 2 – methyl –1, 7–dioxaspiro[5, 5] undecane) may be released by *Goniozus* females during contests which is always released by the loser and aggression in contests is reduced after spiroacetal release.

It was observed that *G. nephantidis* fed on other females, eggs and laid its own clutch when they were released together. The outcome of inter-specific or intra-specific contests is, in general, expected to be related to the costs incurred (Enquist and Leimar, 1990; Payne, 1998), differences in competitive ability between individuals (Grafen, 1987; Hammerstein, 1981; Maynard-Smith and Parkar, 1976), prior ownership (Papaj and Messing, 1998; Peterson and Hardy,1996) and to the resource value (Field and Calbert, 1998) to the competitors.

When more than one female parasitoid was released the fecundity was severely affected because the parasitoids were found attacking each other and disrupting egg laying behaviour of the females. Similar observation was observed in *Parasierola swirskiana* Argaman (Hymenoptera: Bethylidae) while parasitizing on *Batrachedra amydraula* Meyrick (Eitarn, 2001). George & Abdurahiman (1986) reported that female *G. keralensis* Gordh destroys and consumes the eggs of other females when encountered on a parasitized host with her mandibles, but never destroys her own eggs. Venkatraman and Chacko (1961) noted that *G. marasmi* (Kurian) females destroy the eggs and larvae of conspecific females when a parasitized host larva is encountered. The female will subsequently oviposit on the host. The longevity of *G. nephantidis* was adversely affected when more than one female was released which could be due to intra–guild competition while parasitizing the host

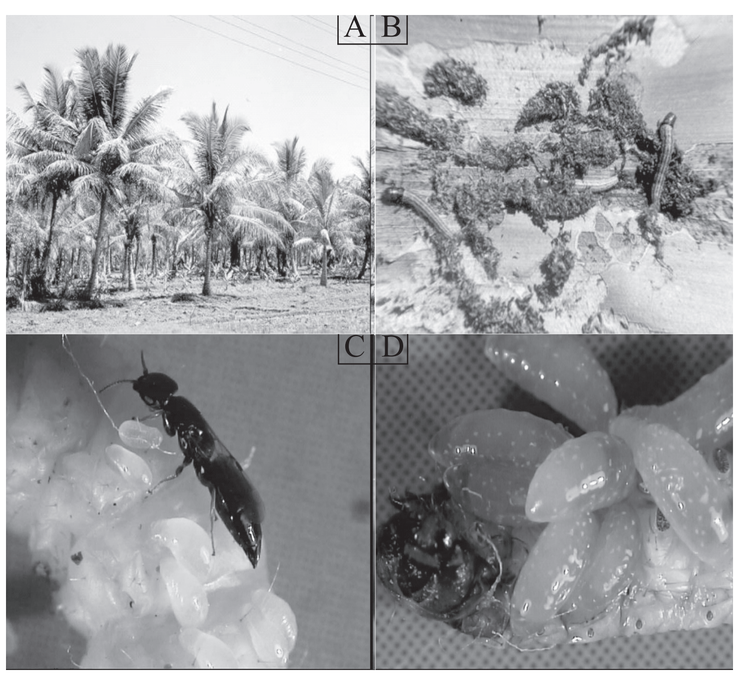

Plate 1. A. Damaged coconut palms, *B. Opisina* larvae feeding on coconut leaves, C. Brood guarding behaviour (parental care) in *Goniozus*, D. Full grown larvae of *G. nephantidis*.

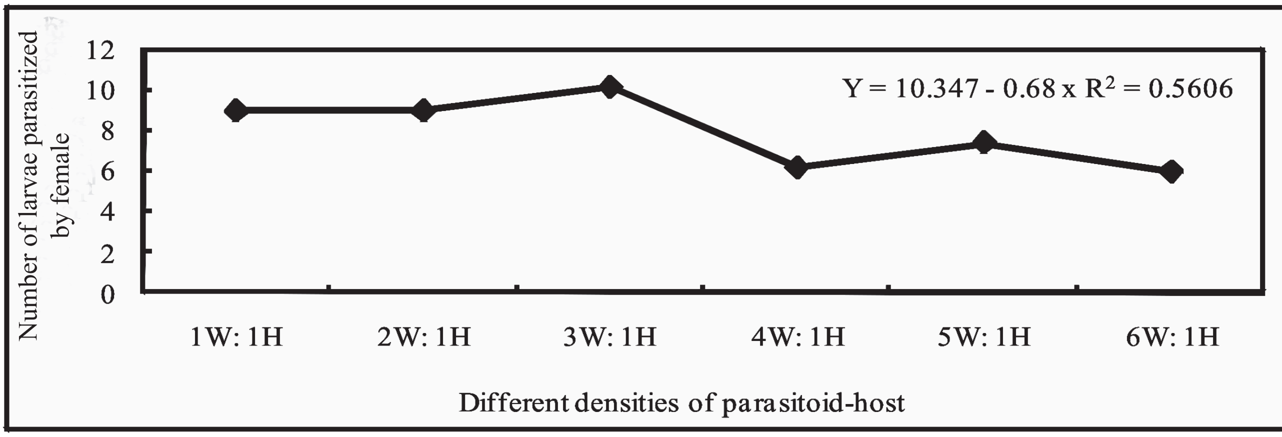

Fig. 4. Relationship between numbers of larvae parasitized per female parasitoid and host-parasitoid density

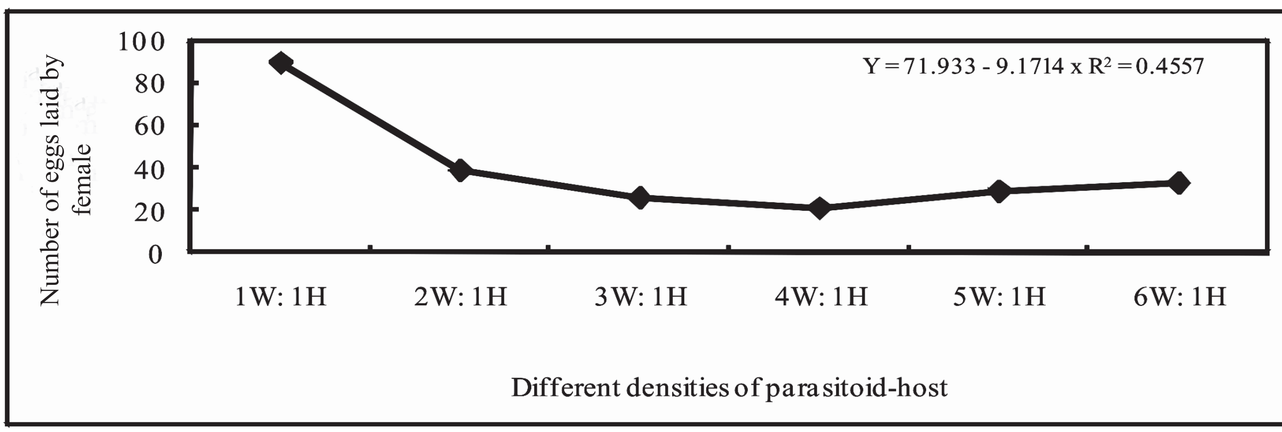

Fig. 5. Relationship between number of eggs laid by female parasitoid and host-parasitoid density

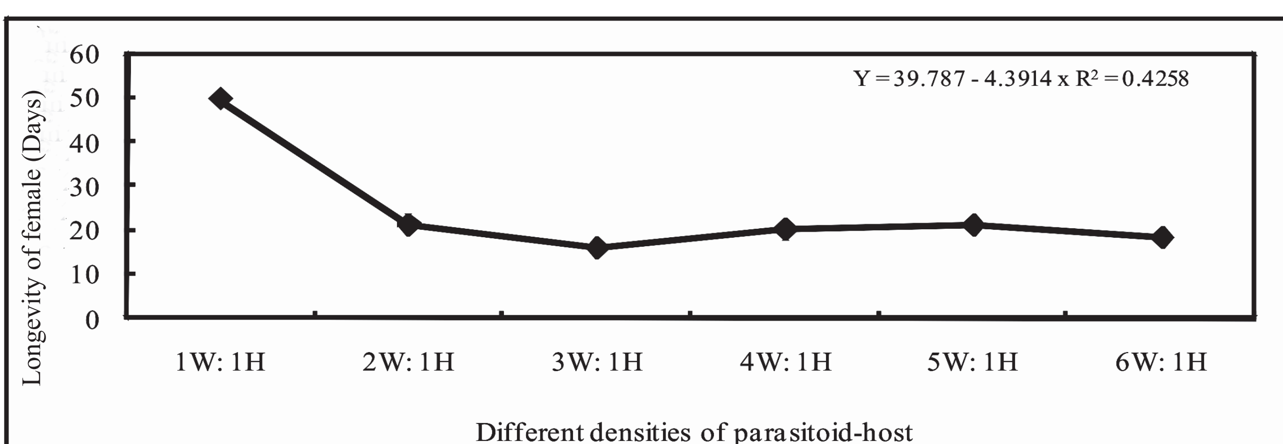

Fig. 6. Relationship between longevity of female parasitoid and host-parasitoid density

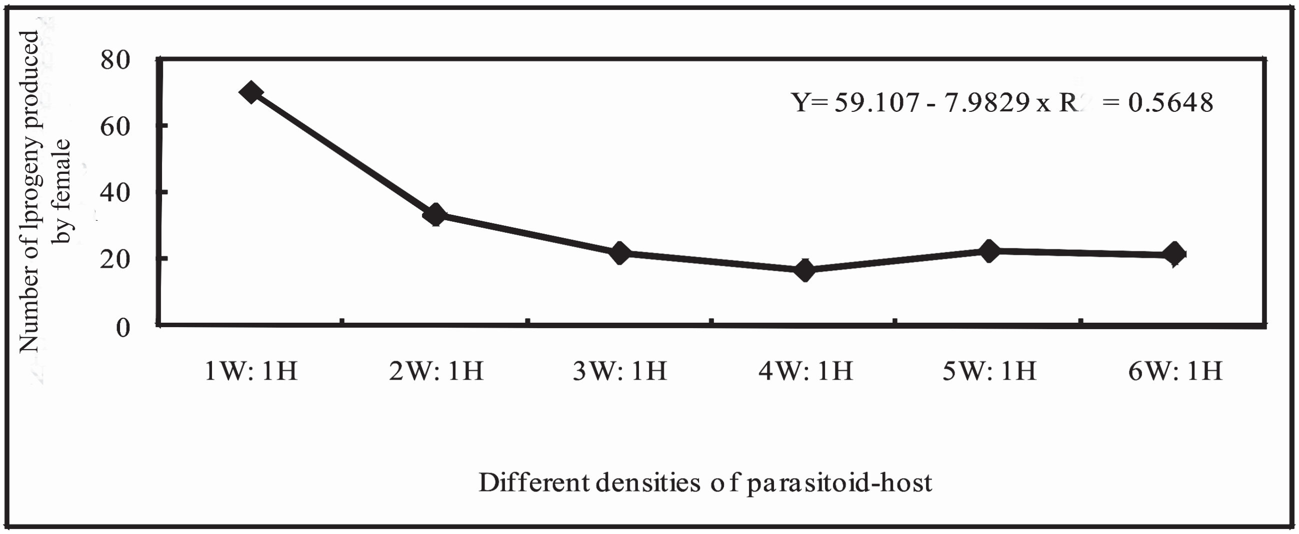

Fig. 7. Relationship between progeny of female parasitoid and host-parasitoid density

larva. *G. nigrifemur* survived for 90 days when exposed to *Pectinophora gossypiella* (Saunders) (Luft, 1996).

The study clearly indicated that either higher densities of the parasitoid to single host or higher densities of the host to the parasitoid did not contribute to an appreciable increase in the efficiency of the parasitoid, its fecundity and longevity. However, a behavioural change was observed which impaired the biological attributes.

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