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Effect of host's larval age on the functional response and associated behavioral activities of the parasitoid

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Abstract

The functional response of interaction between *Campoletis chlorideae* Uchida (Hymenoptera: Ichneumonidae) and different larval stage of the host *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae) at different parasitoid density were studied in entomological laboratory, department of Zoology, D. D. U. Gorakhpur University, Gorakhpur, U. P. in summer season of 1999-2000. The host density increases, the number of antennal encounters of the parasitoid increases significantly in all the host larval age and is maximum in 2nd instar ($y = -3.363+38.178 \log x$, $r = 0.990$, $p < 0.001$) followed by 3rd, Ist, 4th, 5th, 6th instar. With the increase in host density the number of stings by the parasitoid into the host's body increased significantly in all the host larval age and is maximum in 2nd instar ($y = -4.613+33.172 \log x$, $r= 0.989$, $P < 0.001$), 3rd, Ist, 4th, 5th, 6th instar of the host. Analysis of variance shows that the number of antennal encounters and stings was significantly influenced between 6 host age ($F = 16.82$, $P < 0.001$) ($F = 13.85$, $P = 0.001$) as well as between the 7 host density ($F = 7.11$, $P < 0.001$) ($F = 6.809$, $P < 0.001$). As the host density increases the number of offspring emerged increased significantly in all the host larval instar. The functional responses of *C. chlorideae* indicate that this parasitoid could be a candidate for biological control of *H. armigera*.

Keywords: Functional response, *Helicoverpa armigera*, *campoletis chlorideae*, biological control

Introduction

The gram pod borer *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae) is an important pest of chickpea and its causes enormous lossess to this crop (Ravi & Verma, 1997; Nath & Rai, 2000) [1, 2]. The endolarval parasitoid *Campoletis chlorideae* Uchida is an effective biocontrol agent against *H. armigera* and parasitises the moth's larval stages (Sachan & Bhaumik, 1998a; Teggelli *et al.*, 1999; Kaur *et al.*, 2000) [3, 4].

The response of a parasitoid to increased host densities may be through either increasing their own number (Numerical response), or by changing the number of hosts that each individual destroys (Functional response) (Soloman, 1949). The functional response is the response of individual parasitoid to changing host densities. This response is essential for clear understanding and proper approach to the modeling of host-parasitoid-interactions (Huffaker et.al., 1971; Ables & Shepard, 1974) [7, 8] and is considered to be of central importance (Holling, 1966) [15]. The functional response has been thoroughly explored by Lenteren & Bakker (1976) [10]. In such studies, exposure time between the Parasitoid and host is kept constant (Abidi et.al., 1987; Kumar *et al.*, 1994) [11, 37, 12]. Holling (1959) [46] classified the functional response of a parasitoid into three categories (Fig.1); type I, where there is a linear increase to a maximum in the number of hosts parasitized as host density increases, type II, where the response increases non-linearly towards a maximum value, and type III, where the response is sigmoid again approaching an upper asymptote. Type III responses are thought to be more characteristic of vertebrate predator (Holling, 1965, 1966) [15] but they have also been observed with entomophagous invertebrates (Lenteren & Bakker, 1976, Hofsvang & Hagvar, 1983; Kumar *et al.*, 1994) [10, 12,17, 36,25]. The biology and behaviour of *C. chlorideae* has been investigated by several authors but very few works has been made to functional response behavior. Therefore, the Present investigation was aimed to find out the functional response and associated behavioral activities of *C. chlorideae* with different host larval ages.

Materials and methods

Culture - The parasitoid *C. Chlorideae* and its host, *H. armigera* were reared on *Cicer arietinum* Linn (Chickpea) in the laboratory at 22±4^{0}C, 70±10% RH and 10hrs light; 14th dark photoperiod (Kumar *et al.*, 1994) [12]. *H. armigera* possess six larval ages and a pupal stage before becoming adult (Jayaraj, 1982; Tripathi & Sharma, 1984) [18, 19]. The different larval age of the host were drawn from the maintained culture and utilized as hosts. One day old, mated and experienced (T' Hart *et al.* 1978) [20] female parasitoid of *C. Chlorideae,* satiated (Mathavan, 1976) [21] with a 30% honey solution were used in the experiments.

Functional Response - To study the functional response of *C. chlorideae*, one, two, four, eight, sixteen, thirty two and sixty four Ist instar host were placed separately on to moistened filter paper. Each filter paper was transferred individually to troughs (Ca 20 cm diameter x 10cm height) covered with glass plates. One parasitoid was introduced in to each trough and was allowed to attack hosts for 3 hrs.

The different activities of each parasitoid during the experiment were observed by magnifying lens and recorded after the pattern of Kumar *et al.* (1994)[12]. After the commencement of the experiment the larvae were transferred to glass tubes (10x3.25 cm.) with fresh foliage of *C. arietinum* (chickpea) for further development. Each tube was covered with a muslin cloth. After cocoon formation the cocoons were collected and transferred singly by zero number camel hair brush into marked sterilized glass vials (5x1.25 cm.) with leaves of chickpea (Kumar *et.al*., 1994) [12] to provide moisture to the developing eggs (Pandey *et al.*, 1990) until emergence.

The mouth of the glass vials were plugged with absorbent cotton and the cocoons monitored for adult emergence (Abidi *et al.*, 1988) [23, 37]. After emergence the parasitoid were counted. The experiment was replicated five times with new experienced female parasitoid and fresh hosts. The same experiments were performed on the 2nd, 3rd, 4th, 5th and 6th instar of the host *H. armigera.* Because of chance of super parasitisation (Force & Messenger, 1965) [24] or egg larval mortality (Hofsvang & Hagvar, 1975), the resulting number of parasitoid emerged has been taken as a parameter of number of eggs laid in the different host larval ages in the present investigation.

Results

i) Number of antennal encounters of the parasitoid, *C. chlorideae* with the host *H. armigera*

As the host density increases, the number of antennal encounters of the parasitoid increases significantly in all the host larval age and is maximum in 2nd instar ($y = -3.363+38.178 \log x$, $r = 0.990$, $p < 0.001$) followed by 3rd instar ($y = -3.648+36.375 \log x$, $r = 0.988$, $p<0.001$), Ist instar ($y = -4.091+35.284 \log x$, $r=0.989$, $P < 0.001$) and 4th instar ($y = -3.142+27.619 \log x$, $r = 0.989$, $P < 0.001$), 5th instar ($y = -0.179+2.207 \log x$, $r = 0.987$, $P < 0.001$) and 6th instar ($y = 0.150+0.878 \log x$, $r = 0.994$, $P < 0.001$) (Tabel-1, Fig.-2). Analysis of variance shows that the number of antennal encounters was significantly influenced between 6 host age ($F = 16.82$, $P < 0.001$) as well as between the 7 host density ($F = 7.11$, $P < 0.001$) (Table-2).

ii) Number of stings of the host, *H. armigera* by the parasitoid C. *chlorideae*

With the increase in host density the number of stings by the parasitoid into the host's body increased significantly in all the host larval age and is maximum in 2nd instar ($y = -4.613+33.172 \log x$, $r= 0.989$, $P < 0.001$), followed by 3rd instar ($y= -4.742+30.942 \log x$, $r = 0.989$, $P < 0.001$), Ist instar ($y = -4.9703+29.138 \log x$, $r = 0.988$, $P < 0.001$) and 4th instar ($y = -3.942+22.969 \log x$, $r = 0.986$, $P < 0.001$), 5th instar ($y = 0.214 + 1.186 \log x$, $r = 0.986$, $P < 0.001$) and 6th instar ($y = 0.092+0.593 \log x$, $r = 0.988$, $P < 0.001$) of the host (Table-3, Fig. 3). Analysis of variance also revealed that number of stings was significantly influenced between 6 host age ($F = 13.85$, $P = 0.001$) as well as between the 7 host density ($F = 6.809$, $P < 0.001$) (Tale-4).

iii) Number of *C. chlorideae* offspring emerged from parasitized *H. armigera*

The relationship between the number of parasitoid emerged and host density resembled to those of antennal encounters and parasitoid attacked (stung), i.e. the number of parasitoid emerged increased slowly at first, then rapidly to gain a maximum value and thereafter, tend to level (Fig. 4). As the host density increases the number of offspring emerged increased significantly in all the host larval instar. It was observed that no any cocoon formation in the parasitized larvae of 5th and 6th in star of the host *H. armigera* due to the large size, hardness of the host cuticle and defense mechanism of the 5th and 6th instar. The number of emergent's is maximum in 2nd instar ($y = 3.643+13.525 \log x$, $r = 0.934$, $P < 0.001$) followed by 3rd instar ($y = -3.671+12.861 \log x$, $r = 0.933$, $P < 0.001$), 1st instar ($y = -3.499+12.102 \log x$, $r = 0.935$, $P < 0.001$) and 4th instar ($y = -2.764-9.799 \log x$, $r = 0.931$, $P < 0.001$) of the host (Table-5, Fig. 4). Analysis influenced between 4 host age ($F = 31.99$, $P < 0.001$) as well as between the 7 host density ($F = 3.89$, $P < 0.001$) (Table-6).

Table 1: Mean frequency of antennal encounter of the parasitoid *C. chlorideae* at seven levels of host densities of the different larval age of *H. armigera.* Each entry is mean of 5 replicates (mean ± SD)

Initial host density	**Number of antennal encounters**					
	1st instar	**2ndinstar**	**3rdinstar**	**4thinstar**	**5thinstar**	**6thinstar**
1	0.40±0.04	0.8±0.4	0.6±0.48	0.2±0.04	0.2±0.04	0.2±0.04
2	1.8±0.74	2.8±0.748	2.2±1.16	1.2±0.40	0.6±0.48	0.2±0.04
4	15.0±3.03	18.0±3.68	16.2±2.56	12.0±2.82	1.4±0.48	0.6±0.48
8	27.4±2.72	31.2±3.54	29.2±2.99	21.8±3.42	2.6±1.01	1.0±0.63
16	40.0±4.81	45.0±4.56	42.4±2.41	32.0±3.40	3.0±1. 41	1.2.0.40
32	52.2±3.96	57.2±4.53	54.8±2.56	40.4±3.82	3.4±1.01	1.4±0.48
64	57.6±4.31	62.8±4.70	59.0±3.46	45.0±3.40	4.0±2.28	1.8±0.74
Regression : y = a + b log x						
A	-4.091	-3.362	-3.648	-3.142	0.179	0.150
B	35.284	38.178	36.375	27.619	2.207	0.878
R	0.989	0.990	0.988	0.989	0.987	0.994
P	0.001	0.001	0.001	0.001	0.001	0.001

Table 2: Two way analysis of variance of the data Mean frequency of antennal encounter of the parasitoid *C. chlorideae* at seven levels of host densities of the different larval age of *H. armigera.*

Source of variation	**d. f.**	**Sum of squares**	**Mean Squares**	**F Value**	**P**
Between 6 host age	5	10197.65	2039.53	16.82	0.001
Between 7 host density	6	5174.35	862.39	7.11	0.001
Total Interactions	30	3637.23	121.24		
Total	41	19009.23	463.63		

Table 3: Mean frequency of no. of stings of the parasitoid *C. choloridae* at seven level of host densities of the different larval ages of the *H. armigera*. Each entry is mean of 5 replicates (mean±SD)

Initial host density	Number of antennal encounters					
	1st instar	2ndinstar	3rdinstar	4thinstar	5thinstar	6thinstar
1	0.2±0.04	0.6±0.48	0.4±0.04	0.2±0.04	0.2±0.04	0.2±0.04
2	0.8±0.40	1.2±0.74	1.0±0.63	0.6±0.48	0.4±0.04	0.2±0.04
4	9.4±2.05	12.0±2.82	10.6±1.49	6.4±2.15	1.0±0.63	0.4±0.48
8	20.6±3.26	26.2±2.56	23.0±3.28	16.8±3.54	1.4±0.48	0.6±0.48
16	29.0±3.03	35.0±2.28	32.4±2.41	24.0±3.28	1.8±0.74	0.8±0.40
32	40.0±3.40	46.4±2.15	42.8±3.70	31.0±3.40	2.0±0.89	1.0±0.63
64	49.4±3.77	56.0±4.42	52.2±3.96	38.6±2.41	2.2±0.74	1.2±0.74
Regression : y = a+b log x						
A	-4.970	-4.613	-4.742	-3.942	0.214	0.092
B	29.138	33.172	30.942	22.969	1.186	0.593
R	0.988	0.989	0.989	0.986	0.986	0.988
P	0.001	0.001	0.001	0.001	0.001	0.001

Table 4: Two way analysis of variance of the data of Mean frequency of no. of stings of the parasitoid *C. choloridae* at seven level of host densities of the different larval ages of the *H. armigera*

Source of variation	d. f.	Sum of Squares	Mean Squares	F-Value	P
Between 6 host age	5	6524.21	1304.84	13.85	0.001
Between 7 host density	6	3850.04	641.67	6.81	0.001
Total Interactions	30	2826. 86	94.23		
Total	41	13201.11	321.98		

Table 5: Mean frequency of number of offspring’s emerged from parasitoid *C. choloridae* at seven level of host densities of the different larval age of the host *H. armigera.* Each entry is mean of 5 replicates (mean ± SD)

Initial host density	Number of emergents			
	1st instar	2ndinstar	3rdinstar	4thinstar
1	0.2±0.04	0.4±0.04	0.2±0.04	0.2±0.04
2	0.6±0.48	1.0±0.63	0.8±0.40	0.6±0.49
4	1.6±1.01	2.2±1.32	1.8±0.74	1.4±0.49
8	3.6±1.16	4.6±1.72	4.0±1.41	3.2±1.16
16	8.6±1.85	9.4±2.05	9.0±2.28	7.2±2.99
32	15.4±3.42	17.4±4.40	16.0±3.03	11.4±4.49
64	22.0±3.40	25.2±4.24	23.8±3.42	18.6±5.12
Regression: y = a+b log x				
A	-3.499	-3.643	-3.671	-2.764
B	12.102	13.525	12.861	9.799
R	0.935	0.934	0.933	0.931
P	0.001	0.001	0.001	0.001

Table 6: Two way analysis of variance of the data of Mean frequency of number of offspring’s emerged from parasitoid *C. choloridae* at seven level of host densities of the different larval age of the host *H. armigera*

Source of variation	d. f.	Sum of Squares	Mean Squares	F-Value	P
Between 4 host age	3	1224.53	408.18	31.99	0.001
Between 7 host density	6	292.56	48.76	3.89	0.001
Total Interactions	18	226.07	12.56		
Total	27	1743.16	64.56		

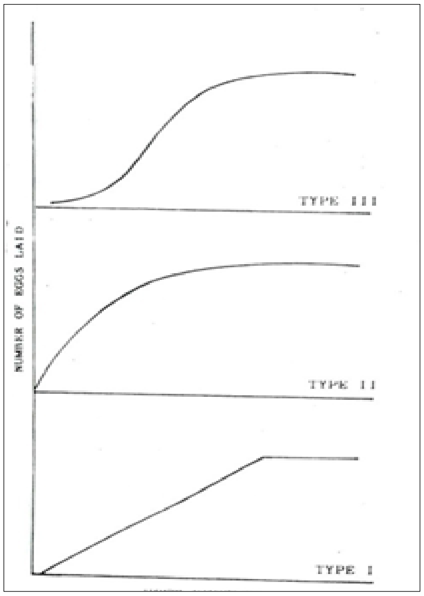

Fig 1: Host Density

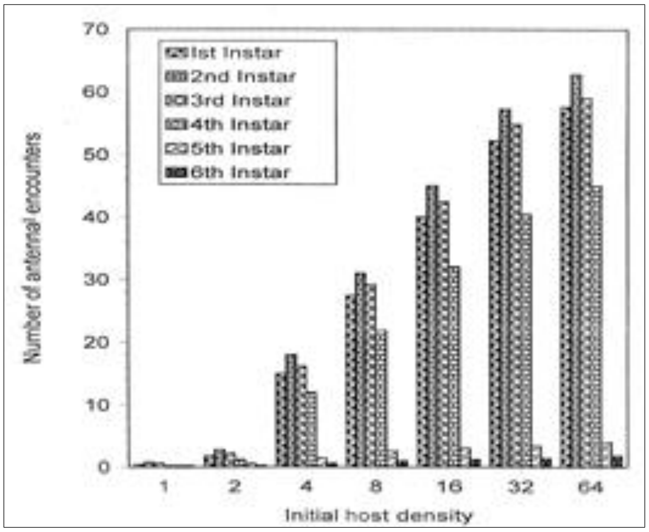

Fig 2: No. of antennal encounters of the parasitoid at seven host density level in different larval age of the host *H. armigera*

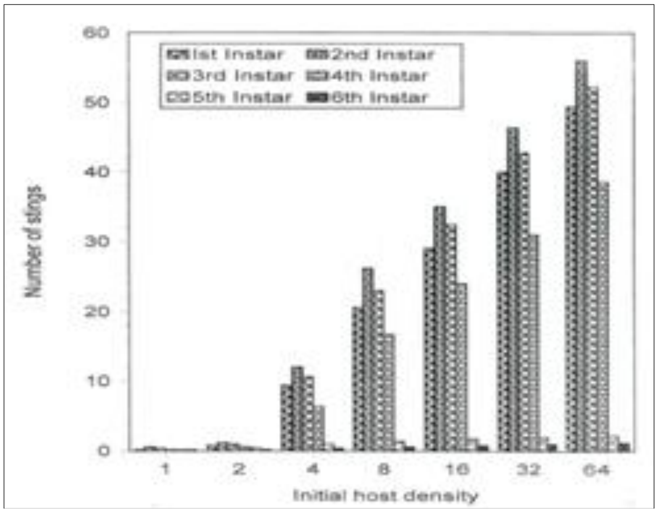

Fig 3: No. of stings of the parasitoid at seven host density level in different larval age of the host *H. armigera*

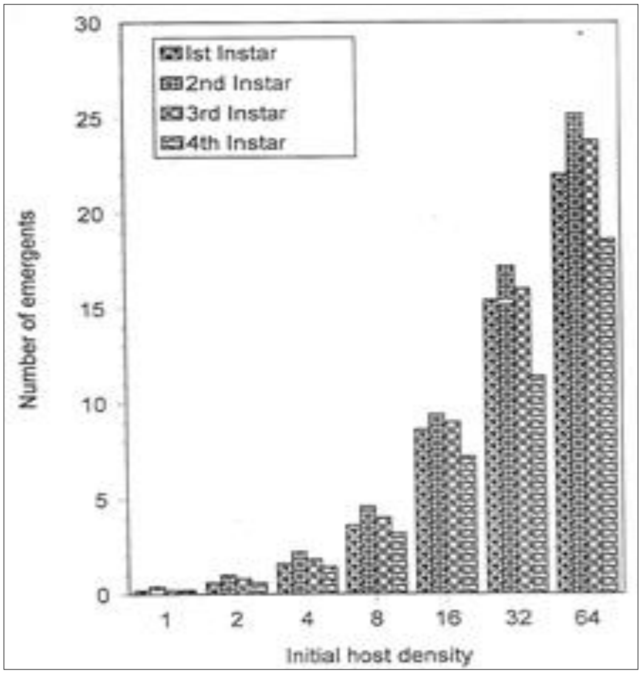

Fig 4: No. of off springs emerged of the parasitoid at seven host density level in different larval age of the host *H. armigera*

Discussion

It was observed that when a female parasitoid *C. chlorideae* approaches the vicinity of the hosts, she becomes active, being to vibrate her antennae up and down and side to side. In doing so she touches the substratum and finally the hosts. As soon as the hosts are encountered by the antennae of the parasitoid she examines them for provisional acceptance or rejection. If the host is acceptable then the parasitisation follows. The number of antennal encounters of the parasitoid was increases significantly by the increase in host density in all the six larval instar. This was possibly due to increased kairomonal concentration, which activates the parasitoid (Nordlung & Lewis, 1976; Ananthakrishnan *et. al.*, 1991) [26]. The kairomones stimulate the host seeking response of the parasitoid, thus play a significant role in host location and host acceptance by the parasitoid (Arthur, 1981) [28, 29]. Kairomones affect the behavior or parasitoid in at least three different ways: (1) By the activation of searching for hosts, (2) Through retention of the parasitoid in the target area and (3) By improving the egg distribution of the parasitoid (Singh & Srivastava, 1990) [30, 45].

The number of antennal encounter was maximum in 2nd instar and followed by 3rd instar, Ist instar, 4th, 5th and 6th instar larvae of the host. Due to the second instar larvae of the host is most preferred the parasitoid *C. chloridae* (Kumar *et al.*, 1994, 2000)[12]. The parasitoid preferred second instar larvae of the host because this stage in addition to having more food than first instar of the host and the hardness of host cuticle, size of the host, kairomonal concentration and defense mechanism of 3rd, 4th, 5th and 6th instar larvae of the host have play an important role in host stage preference by the parasitoid.

The role of increased surface area of contact of the host at higher host densities may play a significant role in increasing of antennal encounters (Hassell & Rogers, 1972; Pandey *et al.*, 1984; Abidi *et al.*, 1987) [32, 11, 37]. The number of antennal encounters might also have increased at higher host densities because the parasitoid spent significantly more time for stinging and parasitisation (Kumar *et al.*, 1988, 1994)[12, 35] since she found there a large number of healthy hosts as she could identify the previously parasitised hosts (Hofsvang and Hagvar, 1983) [17, 36].

The functional response is one of the most important aspects in the dynamics of host- parasitoid interactions (Hassell, 2000) [37]. It has been used to inter basic mechanism underlying the interactions of parasitoid – host behavior, to enhance practical predictive powers for biological control, and even to clarify co-evolutionary relationship (Fan & Petitt, 1994) [38].

With the increase of host density, the number of pricking by the parasitoid in to the hosts body increases significantly in all the larval in stars and is maximum in 2nd instar followed by 3rd, 1st, 4th, 5th and 6th instar of the host. It is due to the increased kairomonal concentration at higher host densities as mentioned earlier which activates the parasitoid (Bouchard & Cloutier, 1985; Abidi *et al.*, 1987; kumar *et al.* 1994)[11, 37, 12]. Kairomones play an important role in host location and host acceptance by the parasitoid. The number of stings was maximum in 2nd instar due to, this stage in addition to having more food than first instar and large host size, hardness of the cuticle and defense mechanism of 4th, 5th and 6th instar of the host. The difference in the number of stinging in different larval instar might be due to presence of varying quantities of the kairmones. Kairomones of the host with a varying attractive potentials for the parasitoid.

Table-2 and Fig. 3 also indicate that it was host density, which influenced the attack pattern of the parasitoid. Similar observations have been reported by T'Hart *et al.* (1978) [20] and Podoler & Major (1981). It has also been observed that not one sting preclude ovipositions at all host densities (Hamilton, 1974; Abidi *et al.*, 1987; kumar *et al.* 1994) [11, 37, 12]. Irrespective of the different larval in stars of the host *H. armigera*.

These false attacks depends upon the host size, stage of development, immediate availability of eggs in the oviduct of the female parasitoid, nutrition of the parasitoid during its development and the co-presence of males along with the females (Abidi *et al.*, 1987; Kumar *et al.* 1988; Tripathi & Singh, 1991) [11, 37, 35].

The behavior of an insect parasitoid, when searching for a suitable host, is guided by a single general principle: The attempt to parasitize as many hosts as possible and thereby achieves maximum reproductive success (Cook & Hubbard, 1977). We observed that, after stinging, the hosts crawled away from the parasitoid. The female parasitoid when approaching the host is attracted towards it. This initial attraction of the parasitoid to the vicinity of the host is mainly due to the odour of the host (Nordlund & Lewis, 1976; Vet & Croenewold 1991) [26]. Once in the vicinity of the host the female parasitoid tries to locate the individual by drumming with its antennae. When there is antennal contact with the host the parasitoid probably receives additional cues, which stimulate oviposition.

It was observed that the parasitoid *C. chlorideae* parasitized 1st to 4th in stars of the *H. armigera*, but no any cocoon formation in 5th and 6th in star of the host due to the large size, hardness of the cuticle and defense mechanism of the older host.

As the cost density increases the number of offspring emerged increased significantly in all the four larval in stars. The relationship between the number of parasitoid emerged and host density showed that parasitoid emergence increases slowly at first, as host density increased. Parasitoid emergence increased most rapidly and there after stabilized (Table-5, Fig.4). The number of emerging offspring is maximum in 2nd in stars followed by 3rd in stars. 1st in stars and 4th in stars larvae of the host. Due to the 2nd in stars larvae was most preferred by parasitoid *C. chlorideae* (Kumar *et al.*, 2000) because this stage in addition to having more food than first in stars and the large size, hardness of the host cuticle and defense mechanism of the third and fourth in stars have play an important role in host stage preference by the paasitoiod (Singh & Srivastava, 1990) [30, 45].

The analysis of variance shows that number of offspring significantly influenced between 4 host age as well as seven host densities (Table-6). The oviposition trend of *C. chlorideae* was sigmoid in nature and resembled the type III curve of Holling (1959)[46]. The sigmoid functional responses are density dependent up to some threshold of host density and may contribute to stability if the average host density falls below this. The maximum egg laying capacity of the parasitoid under the described experimental conditions even in the presence of large number of healthy hosts. This type of density responsive behavior of the parasitoid is considered to be the most stability relationship (Holling, 1965; Lawrence, 1981; Abidi *et al.*, 1987; Kumar *et al.*, 1994)[11, 37, 12, 15].

At lower host densities the parasitoid did not find hosts as frequently, reducing the number of eggs laid at these densities. At higher host densities the parasitoid got activated possibly due to increased kairomonal concentration, which stimulates this behavior (Chiri & Legner, 1982; Wen *et al.* 1991). The chance of the parasitoid successfully locating a suitable host were increased as there was a larger host surface area for the parasitoid to contact, thereby resulting in higher levels of parasitisation (Leteren, 1976).

The results discussed so for reveal that *C. chlorideae* is a potential bio- control agent against *H. armigera* because it has a sigmoid functional response resembling the type III curve of Holling (1959)[46] considered to be the most stabilizing relationship. The functional response and its associated behavioral activities are maximum in 2nd in stars than other in stars. The results suggest that this parasitoid *C. chlorideae* could play a role in the integrated control of different larval in stars of *H. armigera*.

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