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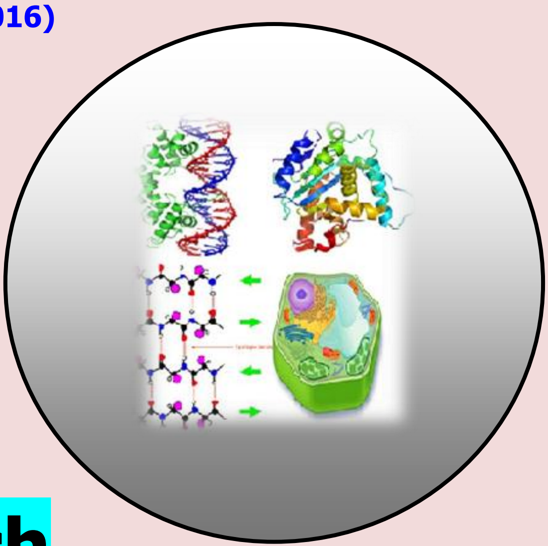

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RESEARCH PAPER

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Effect of Host's Larval Age on Progeny Sex Ratio of Endoparasitoid *Campoletis chlorideae*

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ABSTRACT

The larval endoparasitoid Campoletis chlorideae and its host Helicovepa armigera were reared in the laboratory to determine the progeny sex ratio on different host's larval instars. The sex ratio of C. chloridae is female biased. It is an attribute of potential biocontrol agent. It was observed, that with increase of parasitoid density the proportion of male off springs increase significantly in all the four host larval instars. The sex ratio (number of sons/number of total progeny) was minimum in 2nd instar followed by 3rd instar, 1st instar and 4th instar of host H. armigera. As the host density increases the sex ratio of the off spring in F_1 generation decreases non-linearly with a significant negative correlation and high progeny sex ratio are found at lower host density.
Keywords: Helicoverpa armigera, Progeny sex ratio, Endoparasitoid, Biocontrol, Campoletis chlorideae.

INTRODUCTION

The pod borer *Helicoverpa armigera* (Hubner) is an important pest of chickpea and its cause enormous losses to this crop (Nath and Rai, 2000). The endo larval parasitoid *Campoletis chlorideae* (Uchida) is an effective bio control agent against *H. armigera* (Kaur *et al*., 2000). The *C. chlorideae* helps in suppressing the pest population on chickpea.

An organism can sometimes influence its contribution to future generation by manipulating the sex ratio of its offspring. Sex ratio selection has received much attention from both theoretical and empirical biologist since its initial formulation (Charnove, 1982; King, 1988).

The reproductive strategy of the parasitoid attacking host larval is affected by prevailing conditions for host exploitation (Abidi *et al*., 1988; Kumar et al., 2000). One way to attain this is the control of sex ratio in response to host cues (Hassell, 1986; Abidi *et al*., 1988; King 1996). The sex ratio of the parasitoid is of prime importance when the parasitoid is to be used in a bio-control programme for the suppression of their hosts, as it is the female parasitoid, which brings about parasitisation and mortality of the pest (King, 1998; Colazza and Wajnderg, 1998).

Regulation of the sex ratio of progeny is an important aspect of arrhenotokus species (Avilla and Albajes, 1984). Mated females can lay both haploid and diploid eggs (Waage and Sookming, 1984). Selective fertilization of the eggs in response to external stimuli, like host cues, is the way to control the sex ratio.

Secondary factors may interfere. The depletion of stored sperm, and the aeration of the threshold of stimulation of the spermathecal gland (Flanders, 1965).

The several authors have pointed out that sex ratio of the parasitoid may be an important factor in the biological control programme (Venkateson *et al*., 1999; Kumar *et al*., 2000). Several workers have investigated the effect of host age and size on the offspring sex ratio of the parasitoid (King, 1991; Wang, 1991; Karamauna & Copland, 2000). The present study was initiated to investigate the sex ratio of *C. chlorideae* at varied host's larval age of the *H. armigera.*

MATERIALS AND METHODS

The parasitoid, *C. chlorideae* and its host, *H. armigera* were reared on the *Cicer arietinum* Linn in the laboratory at 22 ± 4^{0}C, 70 ± 10% RH and 10h light: 14 h dark photoperiod (Kumar *et al*., 1994, 2000). The first instars larvae to 4th instars larvae of the host were drawn from the maintained culture and were utilized as hosts. One day old, satiated with a 30% honey solution mated and experienced females (T'Hart *et al*., 1978) were used as parasitoid.

To study the sex ratio of the parasitoid, *C. chlorideae* two sets of experiments were performed.

Experiment 1

In the first set of experiment, 4 troughs (ca 20 cm diameter x 10 cm height) were arranged and numbered as 1 to 4.50 1st instars larvae were placed separately on 4 moistened filter paper and were transferred individually in the marked troughs covered with glass plates. 1,2,4 and 8 parasitoid were introduced in the 1st ,2nd,3rd & 4th troughs respectively and were allowed to attack hosts for 3 hrs. The same experiments were performed on the 2nd, 3rd and 4th larval age of the host.

Experiment 2

In the second set of experiment, carried host densities viz 1, 2, 4, 8, 16, 32 and 64 host were placed on seven moistened filter papers. These filter papers having the hosts were transferred individually in seven differently marked troughs as in the first set through were covered with glass plates. One parasitoid in each petri –dish and was allowed to attack hosts for 3 hrs.

Both the sets of experiments were replicated 5 times with the new experienced female parasitoid and fresh host of different larval age. After parasitisation, larvae of different ages in both the experiments were transferred in the tubes having fresh foliage of chickpea (*Cicer arietinum*) plants (to provide moisture to the developing eggs) until emergence (Kumar *et al*., 1994). The mouth of the glass vials was kept plugged with absorbent cotton.

On emergence the parasitoid were counted sexed and analyzed statistically. The sex ratio of the offspring was calculated as number of males/ number of total progeny. The cocoons that did not yield a parasitoid were not considered (Kumar *et al*., 2000).

RESULTS

The effect of maternal crowding on the progeny sex ratio of *C. chlorideae* was examined. Increasing the number of mothers at fixed 50 host density always increased the progeny sex ratio in all the larval instars. (Table-1, 2) and Fig-1 shows the sex ratio (No. of sons/No. of total progeny) of the parasitoid *C. chlorideae* at fixed host density (50) on the different larval instars of the host *H. armigera* at varied parasitoid density. With the increase of parasitoid density the proportion of sons was increases significantly in all the four host larval stage (Table-1). The sex ratio of offspring in F1 generation is significantly linear increase in different hosts age. This ratio is minimum in 2nd larval instar ($y=0.319+0.373 \log x$, $r = 0.989$, $p < 0.001$) followed by 3rd larval age ($y=0.352+0.374 \log x$, $r = 0.996$, $p < 0.001$), 1st larval instar ($y=0.379+0.369 \log x$, $r = 0.996$, $p < 0.001$,) and 4th larval instar ($y=0.398+0.376 \log x$, $r = 0.995$, $p < 0.001$,) of the host (Table-2, Fig-1) The number of offspring emerged per female parasitoid decrease with the increase of parasitoid density in all the 4 larval instars.

As the host density increases the sex ratio of the offspring decreases significantly in all the larval instars. The proportion of male offspring was maximum in 1 host density and approximately equal in the higher host density (32). The host density increases the proportion of male offspring was significantly decreases in 2nd to 4th larval instars of the host (Table-3). The sex ratio of offspring is minimum in 2nd larval instars ($y=0.844-0.269 \log x$, $r = -0.939$, $p < 0.001$) followed by 3rd larval instars ($y=0.854-0.262 \log x$, $r = -0.948$, $p < 0.001$), Ist larval instars ($y=0.878-0.260 \log x$, $r = -0.936$, $p < 0.001$) and 4th larval instars of ($y=0.922-0.275 \log x$, $r = -0.943$, $p < 0.001$) the host (Table-4, Fig-2).

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DISCUSSION

The sex ratio of the parasitoid is of great biological significance from the point of view of host suppression i.e. the control of the insect pest of the crops (Flanders, 1967). Fisher (1958) postulated a 0.5 sex ratio for sexually reproducing offspring, which was based on the assumption that the natural selection acts to ensure equal parental investment in the production of either sex. Hartl and Brown (1970) and Hamilton (1974) also predicted an equal number of males and females in the population of *Arhenotokous species.* However, distinct variations in female biased sex ratio have been reported (Mackauer, 1976; Abidi *et al*., 1988; Tripathi and Singh, 1990; Shukla and Tripathi, 1993). The observation revealed that the sex ratio of *C. Chlorideae* is female biased. This is an attribute of a potential bio-control agent.

The host's age significantly affect the offspring sex ratio of the parasitoid at varied host and parasitoid densities. Female parasitoid faces a series of challenges before ovipositing her eggs into the host like other insect parasitoid (Vinson, 1976). She must locate the hosts habitat locate the host, assess the host and decide whether to oviposit or not. Female select the correct host species and judge host quality by assessing a number of factors such as shape, size, color, movement and chemical cues. When they select the host, they can also control the gender of the progeny. During ovipositon, the female manipulates the release of sperm from the spermatheca while eggs pass thought her genital tract (Flanders, 1965).

The attraction of the female parasitoid to the host is mainly due to odour of the host (Nordlund and Lewis, 1976; Vet and Groeneworld, 1991). The chemical stimuli (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; Hintz and Andow 1990). The parasitoid *C. chorideae* preferred second instars larvae of the host *H. armigera* (Kumar and Tripathi, 1994; Kumar *et al*., 2000), because this stage in addition to having more food than first instars and quality of food resources emanates more host seeking stimulant. The Kairomone, large size of the host, hardness of the host cuticle and defense mechanism of 3^{rd} and 4^{th} instar of the host was play an important role in the host stage preference by the parasitoid (Vinson and Williams, 1991; Ueno, 1997). Host size is an indication of quality with longer host being better resources but not the too longer ones that may have physiological resistance against the development of parasitic larvae. Parasitoid measure the size of their host's with antennae.

The value of sex ratio was minimum on one parasitoid followed by a marked linear increase at fixed host density (Abidi *et al*., 1988). With the increase of parasitoid density the proportion of sons was increases significantly in all the larval stages (Table-1, Fig-1). It is due to lower mortality of male progeny in super parasitized hosts (Alphen and Nell, 1982; Hofsvang and Hagvar 1983) and adverse in the proportion of diploid eggs laid owing to physical and chemical interference phenomenon (Avilla and Albajes, 1984; Godfray, 1990; Shukla and Tripathi 1993). Vinson (1976), Godfray and Hardy (1990) pointed out the some how many of the parasitoid are unparasitised hosts by detecting factors left behind by the previous parasitoid either externally or internally.

The sex ratio of offspring was maximum at higher parasitoid densities (8 parasitoid at fixed host density 50), probably due to strong mutual interference. The sex ratio of emergent was minimum in 2^{nd} instars and significantly increases to 3^{rd}, Ist and 4^{th} instars (Table-2). The number of emergent per parasitoid decreases with the increase of parasitoid density in all the larval stages. At higher parasitoid density a decrease in the number of hosts per female parasitoid the chances of contamination of the hosts by the parasitoid increases resulting in the deposition of haploid eggs (Suzuki and Iwasa, 1980). This is the basic reason of very high % of the male at the eight parasitoid densities in all the larval instars.

The increase in the sex ratio of the parasitoid with increasing the host density can also been explained on the basis of host contamination phenomenon. As the host density increases the chance of host contamination by the parasitoid decreases resulting in the deposition of more fertilized eggs (King, 1988). The observed increase in the sex ratio of offspring of parasitoid with more hosts available to them the two factors might operate simultaneously: (i) higher host density which increases the rate of parasitisation (Kumar *et al*., 2000) and in this situation the parasitoid oviposits rapidly so that their spermathecal gland, the secretion of which is necessary to activate the sperm, are temporarily exhausted and they lay an increasing proportion of haploid eggs (Flanders, 1962) and (ii) the chance of host contamination is less at higher host number resulting in more female progeny (Kumar and Tripathi, 1987). As a result the value of sex ratio stabilizes (Fig-2). Flanders (1969) tried to explain this phenomenon on the supposition that the movement of the sperm for fertilizing the ovulated haploid egg is regulated by sphincter muscles, which are externally stimulated.

In the present study, observed high progeny sex ratio at lower host densities support the view of King (1987) that parasitic females deposit more haploid eggs at lower host densities than at higher host densities, because the females used to deposit more haploid eggs in shorter oviposition out (Pandey and Singh, 1997). The sex ratio of the offspring was minimum in 2nd instars followed by 3rd, Ist ad 4th instars of the host *H. armigera.*
The knowledge of progeny sex ratio (proportion of male in the population) of parasitoid plays significant role in biological control. Since a significant variation in progeny sex ratio was observed, it helps us to understand the reproductive strategies of the parasitoid and in developing and testing the sex ratio theories and models (Pandey and Singh, 1999). Earlier studies demonstrated that several extrinsic and intrinsic factors influence the progeny sex ratio of parasitoid *C. chlorideae* Uchida (Hymenoptera: Ichneumonidae).

Table 1. Proportion of sons in the total progeny of parasitoid *C. chlorideae* at its four density level on the different larval age of the host *H. armigera*. 50 hosts per trial.

Initial parasitoid density	1st Instar		2nd Instar		3rd Instars		4th Instars	
	T.N. of progeny Produced	% proportion of sons	T.N. of progeny Produced	% proportion of sons	T.N. of progeny Produced	% proportion of sons	T.N. of progeny Produced	% proportion of sons
1	19	36.8	22	30.0	20	34.0	13	38.5
2	28	50.7	31	45.2	29	47.6	15	53.3
4	32	60.6	35	56.0	33	58.8	18	62.2
8	34	70.6	37	63.8	36	67.8	21	73.3

Table 2. Sex ratio (number of sons/ number of total progeny) of the parasitoid *C. chlorideae* at its four density level on the different host larval age (mean ± SD) 50 hosts per trial; 5 replicates per item.

Initial parasitoid density	Sex ratio (mean+- SD)			
	1st Instar	2nd Instar	3rd Instars	4th Instars
1	0.368±0.081	0.300±0.032	0.340±0.017	0.385±0.015
2	0.507±0.060	0.452±0.048	0.476±0.082	0.533±0.101
4	0.606±0.053	0.560±0.042	0.588±0.091	0.622±0.049
8	0.706±0037	0.638±0.038	0.678±0.107	0.733±0.367
Regression: y = a+b log x				
A	0.379	0.319	0.352	0.398
B	0.369	0.373	0.374	0.376
R	0.996	0.989	0.996	0.995
P	0.001	0.001	0.001	0.001

Table 3. Proportion of sons in the total progeny of parasitoid *C. chlorideae* at seven level of host density with one searching female parasitoid on the different larval age of the host *H. armigera.*

Initial parasitoid density	1st Instar		2nd Instar		3rd Instars		4th Instars	
	T.N. of progeny Produced	% proportion of sons	T.N. of progeny Produced	% proportion of sons	T.N. of progeny Produced	% proportion of sons	T.N. of progeny Produced	% proportion of sons
1	0.2	82.5	0.4	77.5	0.2	80.0	0.2	85.0
2	0.6	76.7	1.0	74.0	0.8	75.0	0.6	83.3
4	1.6	75.0	2.2	72.7	1.8	72.2	1.4	78.6
8	3.6	72.2	4.6	79.5	4.0	70.0	3.2	75.0
16	8.6	65.1	9.4	57.4	9.0	60.0	7.2	66.7
32	15.4	45.4	17.2	39.5	16.0	42.5	11.4	47.4
64	22.0	33.6	25.2	30.1	23.8	32.0	18.6	35.5

In addition the sex ratio of the parasitoid depends upon a number of environmental factors including (a) host and parasitoid density (Ashley and Chambers, 1979), (b) post copulatory period following insemination (Mackauer, 1976, (c) variability of the male that inseminates the female (Rabasse and Shalaby, 1980), (d) host size (Charnove and King, 1991; Singh *et al*., 2000),

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(e) host plants (Shukla and Tripathi, 1993) and (f) co presence of males along with the females (Abidi *et al*. 1988). Similarly other factors have been found to be responsible for influencing the offspring sex ratio of the female parasitoid, they are (1) Maternal size, (2) Photoperiod, (3) Relative humidity, (4) host sex, (5) genetic factors, (6) the number of times male has copulated, (7) the closeness to the time of insemination on a short time scale.

Table 4. Sex ratio(number of sons/ number of total progeny) of the offspring of the parasitoid *C. chlorideae* at its Seven level of host density on the different host larval age with one searching female parasitoid; 5 replicates per item (mean ± SD).

Initial parasitoid density	Sex ratio (mean± SD)			
	1st Instar	2nd Instar	3rd Instars	4th Instars
1	0.825±0.400	0.775±0.400	0.800±0.400	0.850±0.421
2	0.767±0.037	0.740±0.389	0.750±0.389	0.833±0.406
4	0.750±0.389	0.727±0.367	0.722±0.027	0.786±0.037
8	0.722±0.027	0.695±0.047	0.700±0.033	0.750±0.389
16	0.651±0.107	0.574±0.029	0.600±0.053	0.667±0.107
32	0.454±0.048	0.395±0.045	0.425±0.064	0.474±0.052
64	0.336±0.208	0.301±0.400	0.320±0.033	0.355±0.023
Regression: y = a+b log x				
A	0.878	0.844	0.854	0.922
B	-0.260	-0.269	-0.262	-0.275
R	-0.936	-0.939	-0.948	-0.943
P	0.001	0.001	0.001	0.001

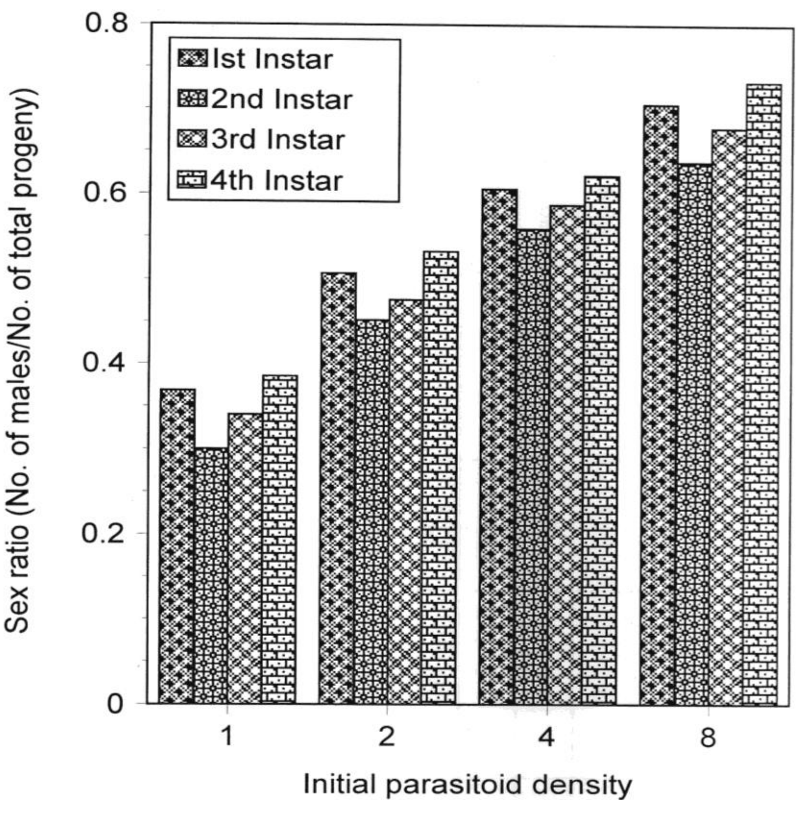

Figure 1. Sex ratio of the parasitoid at its four density level in different larval age of the host *Helicoverpa armigera.*

The results discussed so for reveal that *C. chlorideae* can effectively be used against *H. arigera* as it has a high female biased sex ratio. The progeny production was Maximum in 2nd instars than other instars. For the purpose of obtaining a good female biased sex ratio a small number of parasitoid on the young hosts should be released at any recommended site.

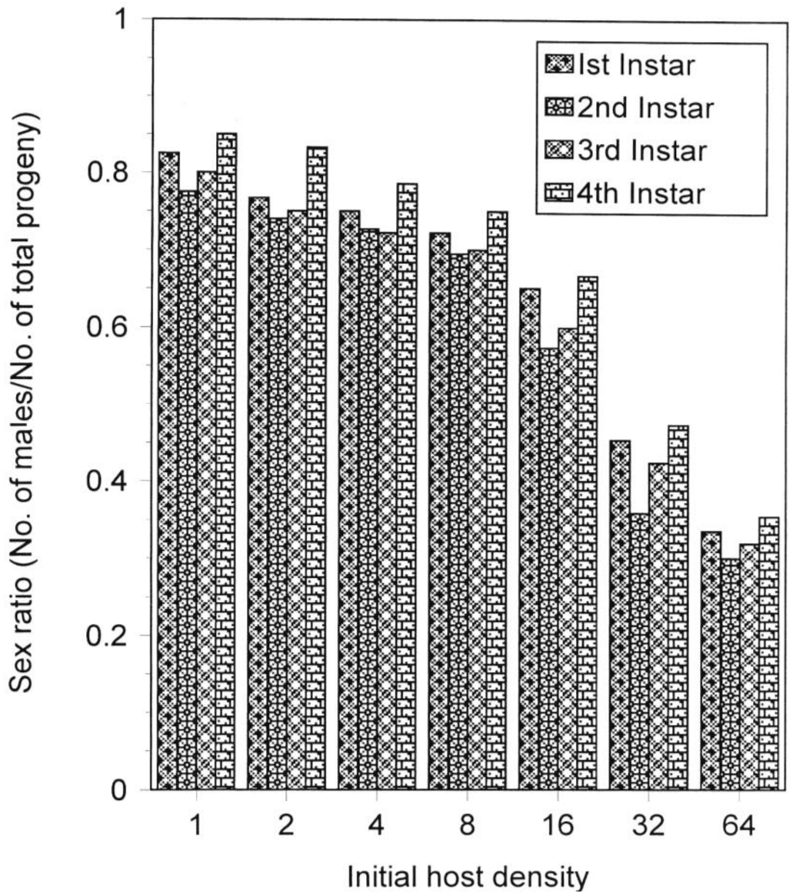

Figure 2. Sex ratio of offspring at seven host density level in different larval age of the host *Helicoverpa armigera* with one searching female parasitoid.

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