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Ecological Studies on *Anagrus incarnatus* Haliday (Hymenoptera : Mymaridae), an Egg Parasitoid of the Rice Planthoppers*

I. Functional Response to Host Density and Mutual Interference

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The functional response to host density and mutual interference of an egg parasitoid, *Anagrus incarnatus* Haliday, parasitizing eggs of *Nilaparvata lugens* (Stål) were analysed. The behavioural response to varying host egg densities of this parasitoid was found to be fitted the Holling's Type II functional response. By utilizing the Holling's (1959) method, the handling time (T_h) and searching efficiency (a) were evaluated. This parasitoid was also found to possess some degree of mutual interference (m), follwing the Hassell and Varley's (1969) model. In addition, observation on the sex ratio of the parasitoid's progeny, with respect to the host egg and searching parasitoid densities available in the present study, showed that its ratio was rather constant, the females usually outnumbered the males, about 2 or 3 to 1.

INTRODUCTION

'Three basic parasitoid responses: (1) the functional response to host density; (2) the response to parasitoid density; and (3) the response to the host distribution, are known to affect searching efficiency of insect parasitoids (Hassell and Rogers, 1972; Hassell and May, 1973). It is known that during given period of time parasitoids (or predators) attack hosts (or prey) at different rates depending on the number of host (or prey) available. A phenomenon in the change in number of attacks per parasitoid (or predator) in relation to the varying host (or prey) densities has been designated as a functional response. This term was originated by Solomon (1949), and later, has extensively been used by Holling (e. g. Holling, 1959, 1961, 1965, 1966). The Hol-

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ling's functional response is recently reviewed by Hasscll (1978). Hassell and Rogers (1972) and Hassell and May (1973) consider mutual interference between searching parasitoids and the response to the host distribution are important in the host-parasitoid interaction and may contribute markedly to stability. Hassell and Varley (1969) developed a model for the mutual interference.

This paper deals with the functional response to host density and mutual interference of an egg parasitoid, *Anagrus incarnatus* Haliday, parasitizing eggs of the brown planthopper, *Nilaparvata lugens* (St&l), under the experimental conditions in laboratory. This work is a part of the study on the biology and ecology of this parasotoid as an important natural enemy of the rice planthoppers in paddy field. The response to the host distribution will be discussed in a separate paper.

MATERIALS AND METHODS

A. *incarnatus* used in this study was from the laboratory stock cultures reared successively on eggs of the brown planthopper. The parasitoid females aged less than 3-h were randomly selected from the stocks and they were allowed to mate prior to be used in the experiments. Eggs of the brown planthopper were used as a host. The experiments were conducted at room temperature, fluctuating between 22°C and 31℃, and averaged 26.4℃ throughout the course of study.

Seven levels of host egg density were used in the experiment and replicated 10 times at each density level. However, number of host eggs in each replicate were not exactly equal due to some technical problems. By nature, eggs of the brown planthopper are usually deposited under the surface of host plant tissue, so their actual numbers could not be counted without dissecting the host plant. Moreover, there are great variations in the number of eggs laid by each individual host over a given period, which could not be controlled. Thus, host density at each level was the average of 10 replicates, in which each replicate eggs were varied within a certain range. They are as follows:

Level	Density (R)	Range
1	6.1	5 - 9
2	21.6	21 - 24
3	34.5	32 - 36
4	43.7	41 - 46
5	53.9	51 - 56
6	62.7	61 - 65
1	95.2	71 - 124

Parasitization of parasitoid was performed in glass tube (2 x18 cm) having both ends open. The rice seedlings bearing host eggs were inserted through one side of the tube and the parasitoid was released on the other side and covered by nylon gauze. After exposure for 24 hours, the rice seedlings bearing host eggs were transferred to the test tube (1.8 x 18 cm) and held for

8–9 days. Thereafter the host plants were dissected to count the number of parasitized eggs. They were then kept in plastic Petri-dish providing with moist filter paper for further development until the state at which sex of parasitoid could be recognized and the sex ratio was then recorded.

For analysis of the data, the Holling's (1959) disc equation was utilized. The equation is:

$$N_a = aTN_t/(1 + aT_h N_t)$$

where N_a = the number of host parasitized,
N_t = the host density,
a = the instantaneous rate of search,
T = the time available for host searching of the parasitoid,
and T_h = the handling time.

Holling (1959) has explained how to obtain the a and T_h by using a linear least squares technique; N_a/N_t is plotted against N_a at each density, the slope of a straight line is equal to $-aT_h$ and the intercept on the ordinate is equal to aT. The goodness of fit between the observed data and the expected number of parasitized eggs obtained from the disc equation was tested by the chi-square method.

For the observation on the mutual interference of this parasitoid, 4 levels of parasitoid density, 1, 2, 4 and 8 females were used in the experiment. Due to the reasons as stated above, the number of host eggs used for test at each parasitoid density were not equal, but allowed to be not greatly different in each replicate and among the different paraisitoid densities. The host densities are as follows:

Parasitoid density	Host density $\bar{x} \pm$ SD	No. of replicates
1	352.4 ± 28.16	5
4	336.8t22.73	5
8	335.6±54.68335.2±46.38	88

For analysis of the data, the Hassell and Varley's (1969) model was utilized. The equation is:

$$a = QP_t^{-m}$$

$$\text{or} \quad \log a = \log Q - m \log P_t$$

where a is the searching efficiency, Q is the 'quest constant', P_t is the parasitoid density and m is the mutual interference.

The value of a at each parasitoid density was estimated by utilizing the formula, of which Hassell (1978) has derived from Nicholson's model:

$$a=\frac{1}{p_t}\log_e\frac{N_t}{N_t-N_a}$$

where N_t is the host density and N_a is the number of host parasitized.

RESULTS

The functional response curve of A. *incarnatus* is shown in Fig. 1. From the curve, it will be seen that this parasitoid attacked more number of host eggs as the density of the latter increased. Rate of attacking increased rapidly as the host density increased, but the curve slightly levelled off at higher host densities. This is probably due to the limitation of egg-laying capacity over the 24-h period of the parasitoid.

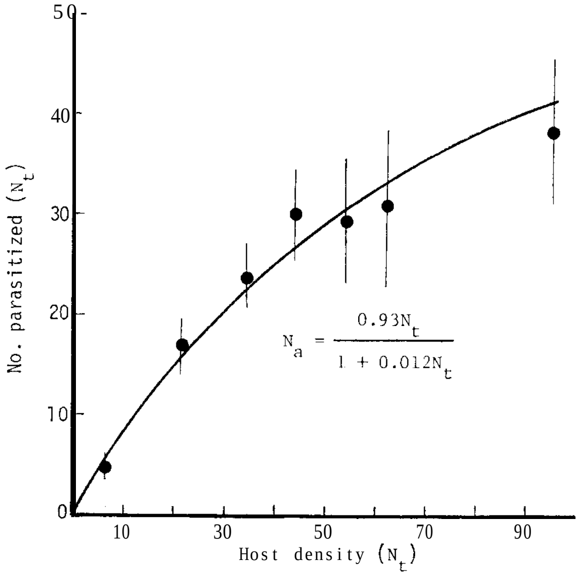

Fig. 1. Functional response of *Anagrus incarnatus* parasitizing eggs of *Nilaparvata lugens* using the Holling's (1959) disc equation. Each point with 95% confidence limits is the mean number of host eggs parasitized at each density level.

Based on the assumption in the Holling's functional responses that parasitoids search and attack the host at random, the goodness of fit between the observed data and the expected parasitized eggs were tested by using the chi-square method. It is shown in Table 1 that the data obtained from the experiment follow well after the Holling's disc equation ($P>0.05$).

From the equation N_a = 0.93 $N_t/(1+0.012$ NJ, the parameters a and T_h were estimated as 0.038 and 0.326, which express in the units of 'hours-" and

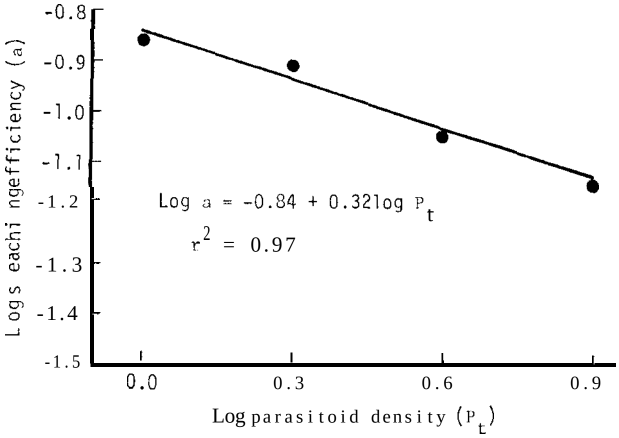

Fig. 2. Interference relationships between the searching efficiency (a) and searching parasitoid density (P,) of *Anagrus incarnatus* parasitizing eggs of *Nilaparvata lugens*.

'hours', respectively.

Fig. 2 shows the interference relationship between the searching efficiency (a) and the parasitoid density (P_t). The results indicate that with increasing of the searching parasitoid density the searching efficiency of individual parasitoid was reduced. This suggests that there was interference among the searching parasitoid females. From the Hassell and Varley's model, the mutual interference (m) was estimated as 0.32.

Sex ratio of the parasitoid progeny obtained from both experiments are shown in Tables 2 and 3. When a single parasitoid female prasitized host eggs

Table 1. 'Test of the hypothesis that eggs of *Anagrus incarnatus* (parasitized eggs) are distributed at random with respect to the host available".

Host density[2]	Per famale parasitoid		χ^2
(N_t)	No. of observed eggs parasitized (N_a)	No. of expected eggs[3] parasitized (N,)	
6.1	5.0	5.3	0.02
21.9	16.6	16.2	0.01
Y4.5	23.7	22.9	0.03
43.7	29.9	27.1	0.29
53.9	29.0	30.4	0.06
62.7	30.6	33.3	0.22
95.2	38.2	41.3	0.23
		(d. f. 6) (P >0.05)	0.86

1) Superparasitism, very few if occurred, was neglected in this test.

2) Host density at each level was the average of 10 samples (see text for explanation).

3) No. of expected eggs parasitized were calculated from the equation, $N_a=0.93\,N_t/(1+0.012$ N,).

Table 2. **Sex** ratio of the progeny of ***Anagrus*** *incarnatus* parasitizing eggs of *Nilaparvata lugens* at different host densities, during 24-h period.

Host density”	Sex ratio2) (Female/Female-i-Male)
6.1	0.67
21.9	0.78
34.5	0.78
43.7	0.78
53.7	0.77
62.7	0.78
95.2	0.78

1) See footnote in Table 1. Experiment was replicated 10 times.

2) No significant difference, by F-test ($P>0.05$).

Table 3. **Sex** ratio of the progeny of *Anagrus incarnatus* parasitizing eggs of *Nilaparvata lugens*, with respect to varying parasitoid densities.

Parasitoid density	No. of host eggs1)	Sex ratio2) (Famale/Male+Famale)
1	**352.4**	0.78
2	**336.8**	***0.64***
4		0.72
8	335.6 335.2	0.70

1) See text for explanation. Experiment was replicated 5 times at parasitoid density 1 and 2 females, 8 times at 4 and 8 females.

2) No significant difference, by F-test ($P>0.05$).

of varying densities, there was no significant difference ($P>0.05$) among the sex ratios of progeny produced in all host density levels (Table 2). In relation to the varying parasitoid densities, again, there was no significant difference ($P>0.05$) in the sex ratios of progeny produced by the parasitoid in all different density levels tested (Table 3). As to the sex ratio of A. *incarnatus*, the females always outnumbered the males, about 2 or 3 to 1.

DISCUSSION

From Fig. 1, the functional responce of ***A.*** *incarnatus* should be categorized as the Holling's functional responses type II (see Holling, 1959 and Hassell, 1978). Hassell (1978) states that type II responses are characteristic of invertebrate predators and parasitoids. In this type of responses, Holling (1959) has pointed out the two crucial components: an instantaneous rate of searching efficiency (a) and the handling time (T_h). The handling time can determine the maximum attack rate over the total time available for search of the parasitoid ($K=T/T_h$). And it was 72 for ***A.*** *incarnatus*. However, Messenger (1968) thought that this value is only of theoretical interest.

For the response of parasitoid to other searching individuals, Hassell and

May (1973) have pointed out that a certain degree of mutual interference (m) may contribute to stability, if its value falls within the range $0<m<1$. The veriety of mutual interference has been observed among the arthropod predators and parasitoids (see Hassell, 1978, for illustrating a number of samples). However, there have been some arguments that if the phenomenon of interference only occurs in a confined space of the laboratory experiments or it is also common under the field conditions. Griffith and Holling (1969) have thought that the interference mainly occurs in the laboratory experiment, so they consider that it is not so important under natural conditions because the encountering parasitoid females will be less frequent in the latter than in the former. Conversely, Hassell and May (1973) consider that we could not say that interference is unimportant under the natural conditions, because in some laboratory experiments parasitoid density is no greater than that often found in the field. Hassell (1971) also reported that some parasitoid species have agressive behaviour. However, Rogers and Hassell (1974) state that the rate of encounters among searching parasitoids will be increased under the confined space of laboratory experiment, but the reduction in searching time will be rather less than under field conditions.

As for the sex ratio of the parasitoid, a somewhat lower female proportion of the progeny produced at lowest host egg density (Table 2) is probably due to fewer host eggs available, resulting the lesser number of fertilized eggs of parasitoid were laid. Sinha and Singh (1979) found that in *Trioxys (Binodoxys) indicus*, an arrhenotokous species, female sex ratio increases as increasing of the host density. In relation to the parasitoid density, Wylie (1965) found that at higher parasitoid density the females of *Nasomia vitripennis*, parasitizing house-fly pupae, produce more number of male progeny.

Mackauer (1976) believes that the reproductive strategy of arrhenotokous species, their natural selection favours a mechanism to produce at least some males to ensure their reproduction. Sex ratio of *A. incarnatus* observed in the present study seems to agree with Mackauer's opinion. Sex ratio of this patasitoid was rather constant, which unlikely affected neither by the host density it ecounters nor the density of parasitoid itself.

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REFERENCES

Griffith, K. J. and C. B. Holling 1969 A competition submodel for parasites and predators. Can. *Entomol.* **101**: *785-818*

Hassell, M. P. 1971 Mutual interference between searching insect parasites. *J. Anim. Ecol. 40*: *473-486*

Hassell, M. P. 1978 *The Dynamics of Arthropod Predator-Prey Systems.* Princeton University Press, New Jersey

Hassell, M. P. and R. M. May 1973 Stability in insect host-prasite models. *J. Anim. Ecol. 43*: 567-594

Hassell, M.P. and D.J. Rogers 1972 Insect parasite responses in the development of population models. *J. Anim. Ecol. 41: 661-676*

Hassell, M. P. and G. C. Varley 1969 New inducive population model for insect parasites and its bearing on biological control. *Nature, Lond. 223: 1133-1137*

Holling, C. S. 1959 Some characteristics of simple types of predation and prasitism. Can. *Entomol. 91:* 385-398

Holling, C. S. 1961 Principles of insect predation. *Ann. Rev. Entomol. 6: 163-182*

Holling, C. S. 1965 The functional response of predators to prey density and its role on mimicry and population regulation. *Mem. Entomol. Soc. Can. 45: 3-60*

Holling, C. S. 1966 The functional response of invertebrate predators to prey density. *Mem. Entomol. Soc. Can. 48: l-86*

Mackauer, M. 1976 An upper boundary for the sex ratio in a haplodiploid insect. *Can. Entomol.* 108 : 1399-1402

Messenger, P. S. 1968 Bioclimatic studies of the aphid parasite *Praon exsoletum. 1.* Effects of temperature on the functional response of females to varying host densities. Can. *Entomol. 100* : *728-741*

Rogers, D. J. and M. P. Hassell 1974 General models for insect parasite and predator searching behaviour: interference. *J. Anim. Ecol. 43: 239-253.*

Sinha, T. B. and R. Singh 1979 Studies on the bionomics of *Trioxys* (*Binodoxys*) *indicus* (Hymenoptera: Aphidiidae) : Effects of population densities on sex ratio. *Entomophugu 24: 289-294*

Solomon, M. E. 1949 The natural control of animal population. *J. Anim. Ecol.* 18: l-35

Wylie, H. G. 1965 Some factors that reduce the reproductive rate of *Nasomia vitripennis* (Walk.) at high adult population densities. *Can. Entomol. 97: 970-977*