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# Effect of Host Density on the Progeny Production of the Egg Parasitoids *Ooencyrtus nezarae* (Ishii) (Hymenoptera: Encyrtidae)

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The effects of host density on progeny production, clutch size and sex ratio of *Ooencyrtus nezarae*, an egg parasitoid of the bean bug *Riptortus clavatus*, were examined to determine the optimal host provision condition in which mass–rearing efficiency of the parasitoid is maximized. Female parasitoids allocated progeny in regard to host density so as to avoid laying more eggs than the host can support. The maximum progeny production and parasitism rate occurred when 5 host eggs were given everyday throughout the life time. However, if we continuously provided with hosts for ten consecutive days, the progeny production with one host per day was more consistent than that with five hosts per day. Female *O. nezarae* reduced the clutch size if the host density was beyond five. However, the overall progeny sex ratio remained constant regardless of the host density. The results suggested that the excessive exposure of the host to *O. nezarae* wouldn't affect the reproductive fitness, but would reduce the reproductive potential of this parasitoid, which can in turn affect the efficiency of mass rearing perspective.

## INTRODUCTION

Progeny production of insect parasitoids is determined by a number of intrinsic and extrinsic factors (Godfray, 1994; Ueno, 1999a, b; Ueno and Ueno, 2007). Host density is one of the determinants affecting many aspects of parasitoid physiology including progeny production and sex ratio (Waage, 1986; Godray, 1994). Hymenopteran parasitoids are known to increase progeny production in response to an increase of host density (Legner, 1967). The number of hosts parasitized per unit time depends on the ability of the individual parasitoids to locate and parasitize a varying number of hosts, i.e., functional response. Also, when many females are present, the number of hosts parasitized is determined not only by their responses to host density but also by their responses to other females, i.e., numerical response (Solomon, 1949; Godfray, 1994). The study of the interaction between parasitoids and hosts may provide information for designing the optimal mass rearing system for biological control programs with parasitoids (Uçkan *et al*., 2004) because increasing host, or parasitoid or both densities should affect the progeny production and sex ratio (Uçkan and Gülel, 1998, 1999).

The encyrtid wasp *Ooencyrtus nezarae* is a small egg parasitoid attacking hemipteran pests in soybean fields (Takasu and Hirose, 1985; Mizutani *et al*., 1996), has a high reproductive capacity, and is easy to rear in the laboratory (Aung *et al*., 2010a, b). This parasitoid is a candidate of biocontrol agents of the bean bug *Riptortus clavatus* (Hemiptera: Alydidae), a serious pest of soybean (Takasu and Hirose, 1985; Honda, 1986). Many studies on the biology of *O. nezarae* have already been made by numerous authors (e.g., Numata, 1993; Takasu and Hirose, 1991, 1993; Aung *et al*., 2010a, b). We have previously demonstrated that the fecundity of female *O. nezarae* strongly depends on the female parasitoid's age (Aung *et al*., 2010b) and host age (Aung *et al*., unpublished). However, the effect of host density on its progeny production remains unclear. This information is of particular importance when we design the effective mass–rearing system of *O. nezarae*. In the present study, we focus on the progeny production of *O. nezarae* in relation to host density and examine whether female *O. nezarae* regulates its progeny allocation in response to host density.

## MATERIALS AND METHODS

Adults of the bean bug *Riptortus clavatus*, a host of *Ooencyrtus nezarae*, were collected in the campus of Kyushu University during the summer season. The collected bugs were returned to the laboratory and were reared in group in plastic cages (22×16×20 cm) at 25±1 ˚Cunder a photoperiod of 16L:8D. The bugs were provided with soybean seeds, seedlings and water. Jute strings were placed in the rearing cages for oviposition sites. Host eggs were collected everyday to obtain hosts of the same age class and were kept in an incubator maintained at 25±0.5 ˚C until use.

Stocks of the egg parasitoid *Ooencyrtus nezarae* were obtained from laboratory cultures maintained at Bioresource and Management Laboratory, Kyushu University. Colonies of *O. nezarae* were maintained as described by Takasu and Hirose (1988). Because the

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size of adult *O. nezarae* largely depended on how many parasitoids were produced from a single host (= clutch size), newly emerged parasitoids with a ratio of 1:3 (male:female) were used for the following experiments to standardize the size of test females. We used one–day–old host eggs for the experiments because host eggs of this age class are suitable for progeny production (Aung *et al*., unpublished).

In the first part, we set up the experiment to observe the effect of host density on the progeny production of *O. nezarae*. A pair of newly emerged parasitoids was put into a test tube (1.5 cm in diameter, 10.5 cm in length) with a droplet of honey, and the tube was kept at 25±0.5 °C, 16L:8D for two days. After the designated period, females were provided with hosts with one of the following densities; 1, 3, 5, 7, or 9. Then, each female in the tube was kept for one day and was allowed to attack the host eggs given. Parasitized hosts were taken out from each test tube on the following day, and were incubated at 25±0.5 °C, 16L:8D until adult parasitoid emergence. The numbers of parasitized hosts and emerged parasitoids were recorded. Progeny parasitoids emerged were sexed to determine the sex ratio. Twenty females were tested for each host density group.

In the second part of the experiment, we observed how female *O. nezarae* responded to host density when the hosts were continuously available. According to the result of the above experiment and preliminary observations, the maximum progeny production occurred at 5–hosts density, and the maximum number of parasitized hosts was five per day. Hence, we set up two types of host density, i.e., 1– and 5–hosts per day. We used four–day–old females for the experiments to observe the ability of female *O. nezarae* to allocate their eggs when they were fully loaded with eggs because, according to our previous findings, the reproductive potential of 4–day–old females was better than females of the other age class and because the maximum egg maturation occurred around day 5 since emergence. The first and second groups of females were provided with one and five hosts, respectively, on the daily basis. During the experiment, honey was given as food. The treatments were repeated for 10 consecutive days. Hosts were kept in an incubator as mentioned above, and the number of progeny emerged was recorded every day. In all, twenty females were used for each group.

## RESULTS AND DISCUSSION

The progeny production of *O. nezarae* gradually increased with increasing host densities, and peaked when host density was five (Fig. 1). The production then decreased when host density was more than 5 per day. Thus, a dome–shaped response was detected (Fig. 1). The maximum number of hosts parasitized occurred at the density of 5 or 7 hosts (Table. 1). Mean clutch size on the other hand decreased with increasing host density if host density was beyond five. However, the progeny sex ratio was not significantly affected by host density ($p<0.05$) (Table. 1).

In the second experiment, the total progeny production, i.e., the total number of progeny produced during a 10 days experimental period, was significantly higher at the density of 5 hosts than that of 1 host ($p<0.001$). Initially, the difference in progeny production at the daily basis was great between the groups. However, the progeny production of the high host density group decreased quickly while that of the low host density group remained constant (Fig. 2). This result suggested that female *O. nezarae* exhausted eggs quickly during 10 days when host density was high.

The present finding has revealed that female *O. nezarae* allocate progeny based on host density. The total progeny production initially increased with increas-

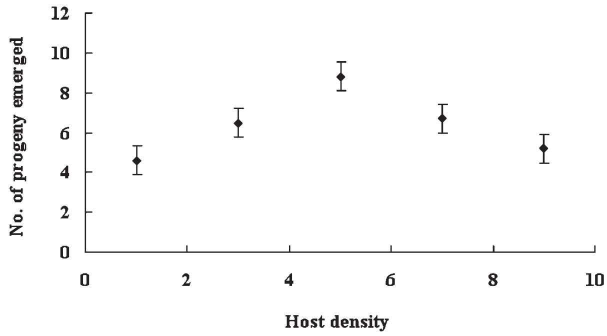


**Fig. 1.** The effect of host density on the progeny production by 2–day–old *O. nezarae*. Data are shown as the mean number ± SE of the total progeny produced per day.

**Table 1.** Effect of host density on parasitization, clutch size and progeny sex ratio of 2–day–old female *O. nezarae* *

| Host density | Mean no. of hosts parasitized | Clutch size | Sex ratio (% males) |
|---|---|---|---|
| 1 | 1a | 4.2±0.2a | 21a |
| 3 | 1.5ab | 4.6±0.2a | 21a |
| 5 | 2.0b | 4.4±0.4a | 20a |
| 7 | 1.9b | 3.4±0.1b | 20a |
| 9 | 1.4ab | 3.5±0.2b | 20a |

* Mean values followed by the same letter within a column are not significantly different (Tukey–Kramer HSD test, $p<0.05$). Data are shown as mean ± SD.

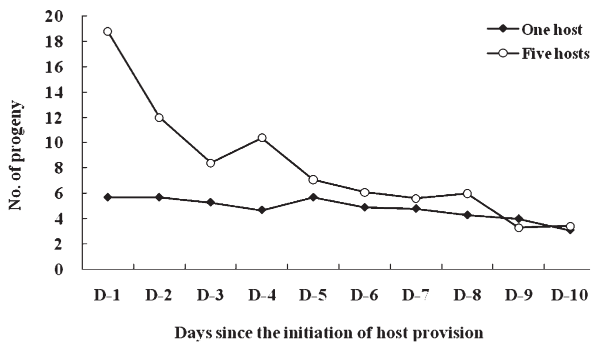


**Fig. 2.** Progeny production pattern of *O. nezarae* at two different host densities during consecutive 10 days.

ing host density (Fig. 1). The result suggests host density should limit the maximum production of the parasitoid progeny. Because clutch size did not differ among host density groups below 5, female *O. nezarae* did not modify the number of eggs laid in each host egg when host density was relatively low. Thus, the progeny production in *O. nezarae* strongly depends on the number of hosts available when host density is relatively low. Likewise, an increase in progeny production may result from increasing numbers of hosts available for parasitization and from the inhibition of superparasitism due to the increase in host density (Hirashima *et al.*, 1990; Godfray, 1994).

Curiously, the total production of *O. nezarae* progeny decreased with host density above 5 (Fig. 1). It is likely that a female can have a fixed number of eggs to be laid during the lifetime, and the fixed lifetime fecundity may explain the limitation and decrease in progeny production with increasing host density (Uçkan and Gülel, 2000); a similar situation is also confirmed for other parasitoid species (Cloutier, 1984; Greenberg *et al.*, 1995; King *et al.*, 1995). A reduction of daily production may indicate that female *O. nezarae* change their reproductive schedule in response to host density; when host density is high, they may extend the oviposition period by reducing the number of hosts to attack in order to spread their eggs among hosts that are present in different patches encountered different days.

When host density was above 5, the clutch size of *O. nezarae* decreased (Table 1). This result suggests that female *O. nezarae* modify the number of eggs laid in each host, reducing the progeny clutch size when host density is relatively high. Numerous authors have reported that parasitoids can adjust clutch size in response to host density. For examples, *Cephalonomia gallicola* (Ashmead), a parasitoid of *Lasioderma serricorne* (F.), lays more eggs on a host when the hosts are rarely encountered; and *Bracon hebetor* regulates the allocation of eggs among hosts by reducing clutch size as host density increases (Hagstrum and Smittle, 1977). Waage (1986) and Charnov and Skinner (1988) also have theoretically demonstrated that the clutch size of a parasitoid should decrease as host density increases. The present finding in our study has shown that female *O. nezarae* can reduce the clutch size if the density is beyond 5 hosts per day.

Two days old females of *O. nezarae* allocate only 4.6 progeny when only one host is available though the maximum number of progeny they can produce is around 8.8 progeny (Table 1). This result means that they do not lay all mature eggs they have, and try to allocate their eggs in future reproductive opportunity. This may support the theory that the parasitoid has a tendency to avoid laying more eggs than the host can support (Milonas and Savopoulou–Soultani, 1999; Yu *et al.*, 2003).

In our study, we did not examine the lifetime progeny production of *O. nezarae* under different host density conditions. However, it is evident that *O. nezarae* quickly reproduces or lays eggs when host density is 5 while the reproductive rate is lower at lower host density (Fig. 2). When host density is above 5, the reproductive rate would be reduced because female *O. nezarae* reduce the number of hosts attacked and the total number of progeny produced (Table 1). Given these results, the maximum progeny production rate should be obtained when host density is around 5. According to the results presented here, we conclude that the appropriate host density for mass rearing of *O. nezarae* will be at five, and this finding may be useful for mass rearing of *O. nezarae*.

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