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https://doi.org/10.5109/22057

出版情報：九州大学大学院農学研究院紀要. 57 (1), pp.115-120, 2012-02. Faculty of Agriculture, Kyushu University
バージョン：
権利関係：

J. Fac. Agr., Kyushu Univ., **57** (1), 115–120 (2012)

Effect of Host–feeding on Reproduction in *Ooencyrtus nezarae* (Ishii) (Hymenoptera: Encyrtidae), an Egg Parasitoid of the Bean Bug *Riptortus clavatus*

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(*Received October 31, 2011 and accepted November 9, 2011*)

The egg parasitoid *Ooencyrtus nezarae* is a candidate for biological control of several hemipterans that are important pests of beans, including *Riptortus clavatus*. However, many aspects of the reproduction in *O. nezarae* remain unknown. The present study highlighted factors affecting the reproduction of *O. nezarae*. When given honey, adult females lived around 40 days, regardless of the presence or absence of the host eggs, or of the age of host eggs. When given honey and young host eggs, females parasitized, on average, around 20 host eggs and produced 75.1 offspring wasps during the lifetime. However, the lifetime offspring production was only 11.2 when 7–day–old host eggs had been given. Female *O. nezarae* was a concurrent host feeder and fed on host hemolymph before oviposition. Although female *O. nezarae* emerged with no mature eggs, they quickly began maturing eggs after emergence, carrying ca. 15 mature eggs within a week. However, the number of mature eggs in the ovary gradually decreased from 15 days after emergence, and 30–day–old females had only 5 eggs, indicating the occurrence of egg resorption in old females. Then, the effect of host feeding on the egg maturation was examined. Although access to host itself caused an increase of egg load of females, manipulation experiments confirmed that host feeding stimulated egg maturation and that female produced ca. 2 additional eggs via a single host meal. The importance of host age and host–feeding in *O. nezarae* reproduction was discussed.

Key words: Biological control, egg production, fecundity, longevity, synovigeny

INTRODUCTION

Adult of many parasitoid species, in particular females, feed on host and non–host foods (e.g., sugar sources) for reproduction and maintenance (Lewis *et al.*, 1998; Jervis *et al.*, 1993; Jervis and Kidd, 1996; Onagbola *et al.*, 2007). Feeding on host material such as host haemolymph is referred as to host–feeding. Host feeding is very common among adult females of synovigenic parasitoids that produce yolk–rich eggs throughout their lifetime, and has been observed for over 140 species across 17 families of Hymenoptera (Jervis and Kidd, 1986) and for several species of parasitic Diptera (Nettles, 1987). Female parasitoids, through host feeding, can gain nutrients that are used to mature eggs (Jervis and Kidd, 1986; Heimpel and Collier, 1996).

Although sugar feeding has been demonstrated to increase the longevity of adult parasitoids in the majority of parasitoid species examined (e.g., Jervis *et al.*, 1993; Fadamiro and Chen, 2005; Fadamiro *et al.*, 2005), some studies have suggested that host meal or haemolymph may be a good source of nutrients for parasitoid survival and fecundity than sugars (Jervis and Kidd, 1986; van Lenteren *et al.*, 1987; Heimpel and Collier, 1996). Although feeding on hosts is essential to maximizing female's fecundity, its contribution to reproduction varies from species to species (Sandlan, 1979; Collier, 1995a; Rivero and Casas, 1999; Ueno, 1999; Rivero *et al.*, 2001; Ueno and Ueno, 2007).

Jervis and Kidd (1986) divided host feeding in terms of its concurrency and destructiveness: concurrent or non–concurrent, and destructive or non–destructive. Concurrent feeding means that female parasitoids use the same host individual for both feeding and oviposition, while non–concurrent means that different hosts are used for the different purposes. Destructive host feeing means that hosts die or heavily damaged upon host feeding, while in the case of non–destructive host feeding, hosts survive or are not damaged. Most evidence implies that host feeding in egg parasitoids always occurs on hosts that are also used for oviposition (Jervis and Kidd, 1986; Takasu and Hirose, 1993). For egg parasitoids, hosts may be important for maximizing both egg production and longevity.

Ooencyrtus nezarae Ishii (Hymenoptera: Encyrtidae) is an egg parasitoid wasp of several phytophagus Hemiptera including the bean bug, *Riptortus clavatus* Thunberg (Takasu and Hirose, 1985, 1986;

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Noda, 1993; Mizutani *et al*., 1996). *R. clavatus* is a serious, widespread pest of soybean in Japan, damaging heavily the pod of soybean. The adult females immigrate to the soybean fields from the surrounding areas and lay eggs singly on leaves, pods and stems of soybean. Chemical control is not always satisfactory, and conservational use of native natural enemies is ideal to lessen the damage caused by this pest. *O. nezarae* is one of the main native egg parasitoids of *R. clavatus*, and is a candidate of conservational biological control. According to the dissection and laboratory experiments, it is a synovigenic species (females emerged from the host without mature eggs) and it used to lay 3–5 eggs with a sex ratio of 1 male: 3/4 females.

The adult wasps of *Ooencyrtus nezarae* feed on natural sugars (sucrose, glucose and galactose) as well as honey (Teraoka and Numata, 2000). The sugars are equally acceptable by the female wasps and do not show any differences in wasp longevity alongside honey (Teraoka and Numata, 2000). However, the situation is a little different with regards to host feeding. *O. necarae* is a concurrent and non–destructive host feeding parasitoid, and, according to our laboratory experiments, host feeding of *O. nezarae* didn't affect host mortality as well as progeny fitness. Females usually feed on host fluid after drilling into the host egg before oviposition (Takasu and Hirose, 1993). Takasu and Hirose (1993) observed that *O. nezarae* accepted to parasitize 0–7 day old eggs of *Riptortus clavatus* but the amount of feeding (feeding bouts) and the number of eggs laid decreased with increasing host age. However, it is unclear whether such effects of host age are associated with the subsequent host acceptance and offspring production. In addition, it is not known whether host feeding in *O. nezarae* can enhance both female longevity and offspring production. Without the information, it is difficult to assess the importance of host feeding in the reproduction of *O. nezarae*. Thus, the current study mainly focused to assess the effects of host feeding on the reproduction, specifically adult longevity, survival, fecundity and egg maturation in the parasitoid. Basing on the present results, we discuss the importance of host feeding in female reproduction of *O. nezarae* and the reproductive strategy of the parasitoid.

MATERIALS AND METHODS

The culture of the host bug *Riptortus clavatus* was established from adult bugs collected at Hakozaki Campus of Kyushu University. The parasitoid *Ooencyrtus nezarae* was obtained from the laboratory culture maintained at Laboratory of Bioresource and Management and was reared as described by Takasu and Hirose (1988). Host *R. clavatus* was reared in plastic cages (22×16×20 cm) providing with water, soybean seeds and soybean seedlings. *R. clavatus* eggs were collected everyday from the cages and were put in the clean plastic cups (6.5×3.5 cm) before experiments to get different host ages. All procedures were made at 25±1˚C with 16L:8D.

Parasitoid longevity, survivorship, fecundity and lifetime fecundity

To assess the effects of host feeding on longevity of *O. nezarae*, we recorded the survival of the females that had been allowed to feed on one of two age categories of the host eggs. In addition, a separate set of the females was prepared without host as a control. Five host eggs of 1–day–old or 7–day–old were attached with vinyl–acetate glue on a piece of filter paper (1 cm^2). A pair of newly emerged male and female *O. nezarae* was placed in each test tube (1.5×10.5 cm) together with a piece of filter paper with 1–day–old or 7–day–old hosts. Honey drop on a piece of parafilm was also placed within the tube to give food for test parasitoids. Then, the tubes were kept at 25±0.5˚C with 16L:8D. Five host eggs were provided daily to each pair of *O. nezarae* until they died and their longevity was recorded. To count the number of parasitized hosts during the lifetime, host eggs given were removed daily from the tube and were transferred to another tube for offspring parasitoid emergence. The tube was kept at 25±0.5˚C with16L:8D, and offspring parasitoids that emerged were checked on the daily basis. Fifteen females each were used for the three treatment groups (control, young and old host groups). The females used for the experiment were standardized in size by selecting the females emerged from a host in 1 male: 3 females.

Egg maturation

The same procedure was done as the above experiment for rearing parasitoids. Females kept with a male were reared at 25±1˚C with 16L:8D. They were not allowed access to host eggs though honey was given as food. Females of 0–30 days old were dissected under a binocular microscope to count the number of mature eggs in the ovary. Twenty females each were dissected for each age class of 0–30 days old.

Effect of host feeding and drilling on reproduction of young and old female wasps

One–day–old female wasps were individually placed in a test tube (1.5×10.5 cm) with a one–day–old host and were allowed to host feed for fifteen minutes without allowing them oviposit. This treatment was possible because females wasps after drilling into a host egg with the ovipositor first feed on host fluids exuded from the hole made on the host surface and, after host feeding, they oviposited in the host egg. After host feeding, test females were divided into two groups. One group was provided with honey for one day and then dissected on the next day to count the number of mature eggs in the ovary. Another group was provided with honey for two days and dissected on the third day. The third group of wasps was set up as the control and was maintained on honey only without host feeding. Twenty females were used for each group.

To assess the effect of female age on egg production versus host feeding, three groups of females of 20 days old were prepared, and the same procedure was applied for these old female wasps. As with the above experiment, twenty females were used for each group.

For the simulation of host drilling on egg maturation of young and old wasps, the same procedures were done as host feeding experiment and we let them to drill without host feeding as well as no oviposition instead of host feeding for both young and old females.

RESULTS

Parasitoid longevity, survivorship, fecundity and lifetime fecundity

The average longevity of female wasps provided with honey only was 40.4 days. On the other hand those that were fed on 1–day–old hosts was 43.7 days while those provided with 7–day–old hosts lived for 39.6 days and there was a statistical difference between the two longevity, but the effect was too small (survival analysis, $p<0.02$) (Table 1). There were no significant differences in longevity between young host and honey ($p<0.06$) as well as old hosts and honey ($p<0.8$), (Table 1). The average life time fecundity of female wasps provided with 1–day–old hosts (on average 75.1 emerged adults) was significantly higher than that of wasps provided with 7–day–old hosts (11.2 emerged adults) ($p<0.05$) (Fig. 1). Similarly, the average number of hosts parasitized by wasps maintained on 1–day–old hosts (20.3) was significantly higher than those parasitized by wasps maintained on 7–day–old host (5.7) ($p<0.05$) (Table 1). Each young host egg produced 3–4 offspring parasitoids whereas each old host egg produced 2 offspring parasitoids.

Table 1. Summary of fecundity and longevity of *O. nezarae*

Types of hosts given	No. of wasps examined	No. of hosts parasitized (Mean ± SD)	Life time fecundity (Mean ± SD)	Longevity (Mean ± SD)
1–day–old hosts	15	20.3 ± 6.6a	75.1 ± 29.5a	43.7 ± 10.4a
7–day–old hosts	15	5.7 ± 2.4b	11.2 ± 6.8b	39.6 ± 8.7b
Control (no host)	15			40.4 ± 5.6ab

Values followed by the different letters in the same column differed significantly($p<0.05$– Tukey–kramer HSD test)

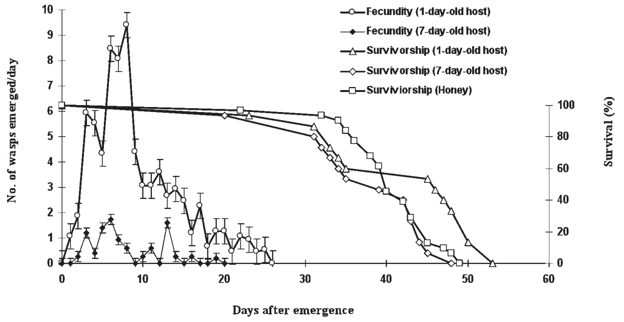

Fig. 1. Survivorship and fecundity schedule of *O.nezarae* (the data shown with mean ± SE).

Egg maturation

The experiment confirmed synovigeny of *O. nezarae*; female *O. nezarae* emerged with no mature eggs and then began producing mature eggs thereafter (Fig. 2). The number of mature eggs increased to reach the peak around day 5 after emergence but declined from 15 days after emergence probably due to egg resorption (Fig. 2). However, the females kept mature eggs in the ovary for the period of 30 days even when no hosts had been available.

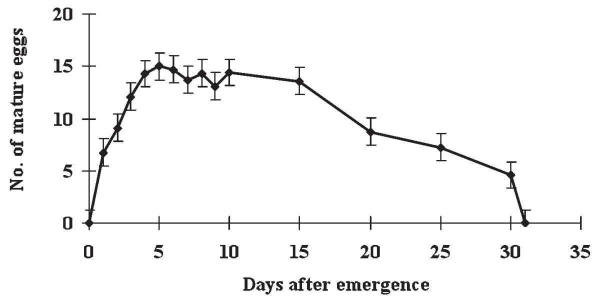

Fig. 2. Egg maturation of *O. nezarae* (the data shown with mean ± SE).

Effect of host feeding and drilling in the reproduction of young and old wasps

The number of mature eggs of 2–day–old wasps maintained on honey for one day after 15 minutes of host feeding (count from start feeding for fifteen minutes under binocular microscope) was significantly higher than those of 2–day–old naïve females ($p<0.05$) (Table 2). Similarly, the number of mature eggs of 3–day–old wasps maintained on honey for two days after 15 minutes of host feeding was significantly higher than those of 3–day–old naïve wasps ($p<0.05$) (Table 3).

Similar results as above were observed with regards to old female wasps, where the number of mature eggs of 21–day–old wasps maintained on honey for one day after 15 minutes of host feeding was significantly higher than those of 21–day–old naïve females ($p<0.05$) (Table 4). The number of mature eggs of 22–day–old wasps maintained on honey for two day after 15 minutes of host feeding was similarly significantly higher than those of 22–day–old naïve females ($p<0.05$) (Table 5). These

Table 2. Effect of host feeding and host drilling on the reproduction of 2–day–old *O. nezarae* females

Types of wasps	No. of wasps examined	No. of mature eggs (Mean ± SD)
naïve females	20	10.0 ± 1.1a
host fed females	20	15.7 ± 0.9c
drilled females	20	14.1± 0.8b

(Mean values with the different letters in the same column of the same group of females are significantly different at $p<0.05$ by Tukey–kramer HSD test)

Table 3. Effect of host feeding and host drilling on the reproduction of 3–day–old *O. nezarae* females

Types of wasps	No. of wasps examined	No. of mature eggs (Mean ± SD)
naïve females	20	11.6 ± 0.8a
host fed females	20	16.2 ± 0.9b

Mean values with the different letters in the same column of the same group of females are significantly different at $p<0.05$ by Tukey–kramer HSD test.

Table 4. Effect of host feeding and host drilling on the reproduction of 22–day–old *O. nezarae* females

Types of females	No. of wasps examined	No. of mature eggs (Mean ± SD)
naïve females	20	7.0 ± 1.5a
host drilled females	20	9.0 ± 1.2b
host fed females	20	11.0 ± 1.6c

Mean values followed by the similar letters in the same column of the same group female are not significantly different at $p<0.05$ by Tukey–kramer HSD test.

Table 5. Effect of host feeding and host drilling on the reproduction of 23–day–old *O. nezarae* females

Types of females	No. of wasps examined	No. of mature eggs (Mean ± SD)
naïve females	20	6.8 ± 2.1a
host fed females	20	11.7 ± 1.5b

Mean values followed by the similar letters in the same column of the same group female are not significantly different at $p<0.05$ by Tukey–kramer HSD test.

results thus show host feeding had a significant effect on *Ooencyrtus nezarae* ovarian development, displayed in the number of mature eggs.

The number of mature eggs of 2–day–old females that had been allowed host access was significantly higher than those of 2–day–old control females (Table 2). Similarly, 22–day–old females that had drilled into a host egg carried significantly more eggs than 22–day–old control females ($p<0.05$) (Table 4).

DISCUSSION

We have shown in the present study that *Ooencyrtus nezarae* can live 1.5 months and lay around 75 eggs during the lifetime under ideal laboratory conditions. Given the relatively long life span and synovigenic egg production in this parasitoid, the availability of food during the adult stage should be important for maximizing the reproductive success. We have designed experiments to separate the effect of host age, feeding and drilling on egg maturation and given evidence that the three factors influence egg production of *O. nezarae*.

The benefits of host feeding are relatively well understood, with a number of studies showing that it can lead to an increase in longevity or egg production (e.g., Jervis and Kidd, 1986; Heimpel *et al*., 1994, 1997; Collier, 1995b; Heimpel and Collier, 1996; Ueno, 1999; Giron *et al*., 2002; Ueno and Ueno, 2007). The influence of host feeding on parasitoid longevity appears to vary from species to species (Jervis and Kidd, 1986). The difference may have to do with interspecific differences in the nature of the nutrients consumed and the amount of sugars present in the ingested fluids (Giron *et al*., 2002). In the current study, host feeding appears to have, if any, a slight effect on longevity of *O. nezarae* because the longevity does not differ among females regardless of the presence of host (Fig. 1). Female *O. nezarae* just sip a small amount of fluids exuded from host eggs before oviposition, and sugars obtained from host feeding should fairly be small in amount. The impact of host feeding on longevity would therefore be small in *O. nezarae*.

The positive correlation between host–feeding and fecundity is well established for many parasitoid species (Jervis and Kidd, 1986; Heimpel and Collier, 1996). In some parasitoids, females cannot produce any eggs, or can produce only a small fraction of the maximum number of eggs, when host–feeding is not allowed (Leius, 1962; Ueno, 1999). In the current study, we have demonstrated that host–feeding has a significant positive effect on egg production by *O. nezarae* females. The results are in line with those obtained in other parasitoid species (Jervis and Kidd, 1986; Heimpel and Collier, 1996).

Curiously, female age has a significant effect on how many eggs *O. nezarae* females can produce from each host–feeding meal. The decrease in fecundity in relation to age may be due to the decreasing physiological activity related to aging and parasitization capability of females. Alternatively, females may feed on a fewer amount of host materials during host feeding when they are older. The declining fecundity period also varies with the type of species (Melton and Browning, 1986; Orr and Boethel, 1990). Although female's age affect egg maturation, in the present study, we do not yet examined which factors influence the decrease in egg maturation with increasing host age of *O. nezarae*.

In addition, our study detected a significant effect of host age on the lifetime offspring production of *O. nezarae*. Host age has been reported to have large effects on feeding, resting and oviposition behavior of *O. nezarae* (Takasu and Hirose, 1993). In their study, the number of feeding bouts and eggs oviposited by *O. nezarae* decreased with increasing host age. The reduced lifetime fecundity and oviposition with host age appears to be linked to progressive reduction of host nutrients available to the female wasps as hosts advance in age. These wasps feed on the yolk or hemolymph of the host eggs which are progressively reduced as the host embryo develops (Takasu and Hirose, 1993). Thus, it is considered that the lifetime offspring production is greatly reduced because female *O. nezarae* take a limited amount of host fluids from old host eggs. Life time fecundity and the numbers of eggs produced were significantly higher in the wasps maintained on 1–day–old hosts than those on 7–day–old hosts. The observation that egg maturation in *O. nezarae* is more rapid in the presence of younger host stages follows earlier reports that imply that a number of gregarious egg parasitoids allocate eggs they lay on the basis of host age and quality (Lewis and Redlinger, 1969; Parker and Pinnell, 1974; Pak and Oatman, 1982).

Many studies focusing on host–feeding have neglected the effect of host access on egg maturation in parasitoids. According to the finding of Morales and Rojas (1996), *Catolaccus grandis* (Burks) females with oviposition experience produced 4 times as many eggs as did inexperienced females while adult nutrition was also important for egg production after host contact. Thus, there can be an interactive influence to egg maturation between host–feeding and host availability.

The present study has designed an experiment to separate the effect of host feeding and drilling (= host access) on egg maturation in *O. nezarae*; our results have shown that not only host feeding but also host access (drilling) itself have a significant effect on the egg maturation of the female parasitoids. When a comparison is made between females without access to host eggs and those with prior host–feeding experience but without oviposition, the numbers of mature eggs they carry are 11.6 and 16.2, respectively, when they are 3 days old. Basing on this result, it might be concluded that 4.6 eggs can be produced via a single host meal. We have made an additional experiment, which gives a striking result that egg load increases after female *O. nezarae* had just prior contact with one host egg; the females carry 14.1 mature eggs while 10.1 and 15.7 eggs are found for control and host–fed females, respectively. Hence, host access itself is a factor causing an increase of egg load, and this effect should be taken into account when the effect of host–feeding is assessed. The result suggests that female *O. nezarae* can add only 2 eggs via a single host meal. The value is small but reasonable because this parasitoid is a concurrent host–feeder that must take only a small amount of host fluids from a single host egg. Similar results have been obtained with old females.

In conclusion, although host feeding had no appreciable effects on *O. nezarae* longevity and survivorship, it had a significant effect on the female life time fecundity and reproduction. With these findings, the factors influencing egg maturation dynamics, other than host feeding, need to be assessed for this parasitoid species. In particular, the effects of direct and indirect host stimuli as well as oviposition should be determined. This will enable us to develop a general theory on how hosts influence reproduction in this and related egg parasitoids.

ACKNOWLEDGEMENT

We thank Ministry of Education, Culture, Sports, Science & Technology (MEXT), Japan and Kyushu University foundation for supporting research and academic study.

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