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Effect of Temperature on Lifetime Reproduction of the Egg Parasitoid Ooencyrtus nezarae (Ishii) (Hymenoptera: Encyrtidae)

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Parasitoid reproductive biology is one of the central issues in biological control with parasitoids because the successful production of parasitoids is essential to mass—rearing of effective biocontrol agents. Parasitoid's fecundity can be influenced by several physical factors, and temperature is an important factor among them. *Ooencyrtus nezarae* is a common egg parasitoid attacking several hemipterans including the bean bug *Riptortus clavatus*, a serious pest of soybean, and is a candidate agent for biological control of soybean pests. In the present study, the lifetime reproduction of *O. nezarae* was examined under different temperature conditions. *O. nezarae* was able to parasitize host eggs at a wide range of temperatures from 20 to 30 °C, and the highest mean fertility, i.e., the maximum progeny production, was around 75.0 at 25 °C. However, the lifetime production of progeny was largely reduced at 20 and 30 °C conditions (33.5 and 36.0 parasitoid progeny, respectively). Parasitization was also affected by temperature; the lowest parasitism rates occurred at 20 and 30 °C. The parasitism rate at 25 was 20.3%, and was significantly higher than those at other temperature conditions. However, temperatures within the range of 20–30 did not significantly alter the progeny sex ratio and clutch size of *O. nezarae*. The results suggested that 25 °C was the optimal temperature for efficient mass rearing of *O. nezarae*

INTRODUCTION

Reproduction in parasitoids has been of great interest in biological control because it is a major component of their life history, the important basis for exploring beneficial parasitoids as natural enemies of pests (Price, 1973, 1974; Quicke, 1997; Ueno, 1999a, b; Papaj, 2000). Knowledge of the reproductive capacity of parasitoids is, in particular, fundamental for the evaluation of a biological control agent's potential (Jervis and Kidd, 1996). Reproductive capacity of parasitoids is influenced by physical factors such as temperature, humidity and photoperiod (Denlinger, 1985; Ratte, 1985; Quick, 1997). Progeny production and adult longevity are two of the major factors determining the reproductive capacity of parasitoids (e.g., Andrewartha and Birch, 1954; Syme, 1975, 1977; Harrison et al., 1985; Tingle and Copland, 1988, Ueno, 1998; Aung et al., 2010a, b).

Progeny production by parasitoids can be estimated by examining their fecundity (the total number of laid eggs or number of eggs in the ovary) or with the fertility (the number of viable progeny) (Jervis and Kidd, 1996). However, the fecundity and fertility of parasitoids are variable features that are influenced by a plethora of intrinsic and extrinsic factors (e.g., Ueno, 1999a, c; Papaj, 2000; Ueno and Ueno, 2007; Aung et al., 2010a). The evaluation of a parasitoid's reproductive capacity there-

fore requires a thorough study of the main effects and possible interactions of such factors on parasitoid fecundity and fertility (Jervis and Copland, 1996). In the case of endoparasitoids, however, fecundity is relatively difficult measure because the eggs are laid inside the bodies of hosts. Moreover, fertility is a more reliable criterion to evaluate the reproductive capacity of parasitoids because it represents the net number of progeny after elimination of individuals that fail to complete development (Jervis and Copland, 1996). Thus it is preferable to study fertility rather than fecundity in endoparasitoids upon the evaluation of their reproductive potential.

OoencyrtusnezaraeIshii (Hymenoptera: Encyrtidae) is a gregarious egg endoparasitoid wasp of several phytophagous Hemiptera including the bean bug, Riptortus clavatus Thunberg (Takasu and Hirose, 1985, 1986; Noda, 1993; Mizutani et al., 1996). It is a good candidate agent for biological control of hemipteran pests of soybean like the bean bug (Takasu and Hirose, 1986; Mizutani et al., 1996). This parasitoid is a synovigenic species, and the females emerge from the host egg without mature eggs (Aung et al., unpublished). Our previous study (Aung et al., 2010a) examining the effect of temperature on estimated fecundity (egg maturation) has shown that a delay of peak for egg maturation occurs with decreasing temperatures and that the maximum egg maturation occurs at 20 °C. However, the effect of temperature on the actual fertility (progeny production) during the lifetime remains unclear. Accordingly, the current study was made to focus on the effect of temperature on progeny production, parasitization rate, clutch size and sex ratio of O. nezarae in order to separate the effect of temperature on estimated fecundity (egg maturation) and actual fertility of the parasitoid.

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MATERIALS AND METHODS

Adult bug *Riptortus clavatus*, a host of *Ooencyrtus nezarae*, were collected in the campus of Kyushu University during the summer season. The collected hosts were returned to the laboratory and were reared in plastic cages $(22\times16\times20~\text{cm})$ at $25\pm1~\text{°C}$ under a 16L:8D photoregime. The bugs were provided with soybean seeds, seedlings and water. Jute strings were also provided for ovipositional sites. Host eggs were collected everyday in order to obtain hosts of the same age class and were kept at $25\pm0.5~\text{°C}$ until use.

Stocks of *Ooencyrtus nezarae* were obtained from the laboratory cultures maintained at Bioresource and Management Laboratory, Kyushu University. *O. nezarae* was reared with eggs of the bean bug, and the culture of the parasitoid was maintained as described by Aung *et al.* (2010b). One pair of adult *O. nezarae* was taken from the culture and was put into a test glass tube (1.5 cm diameter and 10.5 cm long) with one *R. clavatus* egg (1–day–old), which was glued on filter paper. The tube was kept at 25±0.5 °C under 16L:8D for one day for parasitization. After parasitisation, host eggs were singly placed in glass tubes, and were reared until parasitoid emergence. The parasitoids emerged from one host with a ratio of 1 male: 3 females were used for the experiment.

On the day of emergence, each pair of newly emerged parasitoids was put into a test tube that contained 5 host eggs and a droplet of honey. Then, the test tubes containing a pair of parasitoids with hosts were placed at one of the following five different temperature conditions (20, 22.5, 25, 27.5 or 30 $^{\circ}$ C). Five young hosts were provided every day, and honey was exchanged once every three days until the female parasitoids died. Thus, the lifetime reproduction of the female *O. nezarae* was examined.

Host eggs were collected from the tubes and were reared as mentioned above. The numbers of emerged progeny and parasitized hosts, and progeny sex ratio were recorded. Twenty females were used for each temperature treatment.

RESULTS AND DISCUSSION

Ooencyrtus nezarae was able to parasitize host eggs at all temperatures ranging between 20 to 30 °C. However, the progeny production was reduced at low and high temperature conditions (Table 1). The number of progeny differed significantly among temperature groups (p<0.01), indicating that temperature had a significant effect on the fertility of O. nezarae. The highest mean fertility, i.e., the maximum progeny production, was observed at 25 °C (Table 1). Also, parasitization was affected by temperature; parasitism rates (= the number of host eggs parasitized per 5 host eggs) were low at 20 and 30 °C (Fig. 1). The maximum number of parasitized host eggs was 20.3 ± 6.6 at 25 °C, and was significantly higher than those at other temperatures (p<0.01) (Fig. 1). However, temperature had no significant effects on progeny sex ratio and clutch size (p>0.05) (Table 1).

Table 1. Effect of temperature on lifetime reproduction of *O. nezarae*

Temperature	No. of progeny (mean ± SD)	Clutch size	sex ratio
20 °C	33.5±6.9a	4.5a	21a
$22.5^{\circ}\mathrm{C}$	$47.0 \pm 7.3 b$	4.2a	20.5a
$25^{\circ}\mathrm{C}$	$75.0 \pm 20.3 c$	4.0a	20a
$27.5^{\circ}\mathrm{C}$	$54.0 \pm 12.8 b$	4.4a	21a
$30^{\circ}\mathrm{C}$	36.0±6.6a	4.6a	19.5a

Mean values followed by the different letters within a column are significantly different at p<0.05 by Tukey–Kramer HSD test.

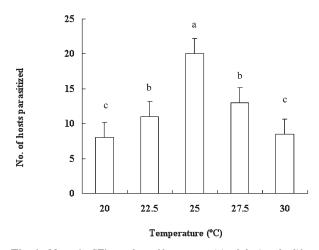


Fig. 1. Mean (\pm SE) number of hosts parasitized during the lifetime of *O. nezarae* reared at different temperatures. The bars capped with different letters differed significantly (p<0.01, Tukey–Kramer HSD test).

Temperature is one of the most important environmental factors influencing physiology and behavior of insects including parasitoids (Ratte, 1985). A common pattern for the relationship between temperature and parasitoid fertility is that lower fertility is observed at extreme temperatures with higher fertility at moderate temperatures (Force and Messenger, 1964; van Lenteren et al., 1987). Thus, the general presumption is that parasitoid cannot mature their eggs or are unable to oviposit outside a range of tolerable temperatures (Force and Messenger, 1964; Greenfield and Karandinos, 1976).

Many studies have shown that rising temperature reduces longevity and fecundity of parasitoids (Sagarra et al., 2000; Matadha et al., 2004) or the fecundity peaks at medium temperatures (Seal et al., 2002; Agboka et al., 2004; Foerster and Butnariu, 2004; Matadha et al., 2004). The current study is in line with the previous findings for other parasitoids, and the maximum fertility in O. nezarae occurs at the moderate temperature, 25 °C. Although our previous finding showed that the maximum egg maturation (estimated fecundity) occurred at 20 °C, the current results revealed the actual fertility, i.e., the highest progeny production, occurs at 25 °C. This may be due to low oviposition activity, which occurs at

the outside range of tolerable temperatures (Force and Messenger, 1964; Greenfield and Karandinos, 1976). Alternatively, long–term maintenance of the mature eggs may be affected at lower temperatures. At least, the reduced fertility in *O. nezarae* would be due to failure of oviposition of all mature eggs at low temperatures. In any case, our study indicates that 25 °C is the optimal temperature for maximizing the mass–rearing efficiency of *O. nezarae*.

The number of mature eggs in the ovary (egg load) can influence many aspects of parasitoid biology and ecology, such as foraging behavior, searching efficiency and motivation to oviposit (Collier et al., 1994; Collier, 1995; Heimpel and Rosenheim, 1998; Ueno, 1999a), which should in turn influence parasitoid and host population processes. Revealing the life history of parasitoids has been the primary approach to evaluate their importance and effectiveness as natural enemies against insect pests (Jervis and Kidd, 1996; Hawkins and Cornell, 1999). However, environmental factors, e.g., temperature, can limit the effect of egg load on parasitoid behavior and ecology; our study suggests the highest fecundity (egg load) in O. nezarae at 20°C conditions does not necessarily lead to the highest realized progeny production, i.e., fertility. Thus, it is important to evaluate the interactions among environmental factors, physiology and behavior of parasitoids when we assess the reproductive potential of parasitoids in biological control programs.

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