中華昆蟲 12: 193-199(1992)
Chinese J. Entomol. 12: 193-199(1992)

Ovipositional Mechanism of an Ecto-parasitoid, *Goniozus legneri* Gordh (Hymenoptera: Bethylidae)

How-Jing Lee Department of Plant Pathology & Entomology, National Taiwan University, 1 Roosevelt Road, Sec. IV, Taipei, Taiwan, R.O.C.

ABSTRACT

Goniozus legneri Gordh is a gregarious ecto-parasitoid of the navel orangeworm, *Amyelois transitella* (Walker). *G. legneri* was able to attack any larval stage of a substitute host, *Anagasta kuehniella* (Mediterranean flour moth) and regulated the number of eggs laid on the host. There was a linear relationship between the host body mass and the number of parasitoid eggs laid. If extra eggs were artificially added to the host, the survival of the parasitoid decreased accordingly. Although the actual ovipositional mechanism is unclear, the volume of injected venom to paralyze a host was not taken into account for the information to determine the number of eggs to be laid. Female parasitoids massage the paralyzed hosts to expel gut contents in order to provide a contaminant-free environment for the offspring. However, the mother perform ed no elaborate maternal care behavior, such as picking up dislodged eggs or larvae and replacing them on the host.
Key words: *Goniozus legneri*, ovipositional mechanism, ecto-parasitoid.

外寄生蜂 *Goniozus legneri* Gordh(膜翅目: 蟻形蜂科)的產卵機制

李後晶 國立台灣大學植物病蟲害學系 台北市羅斯福路四段1號

摘　要

群聚性的外寄生蜂(*Goniozus legneri*)可寄生在代用寄主地中海麵粉蛾(*Anagasta kuehniella*)的任一幼蟲期上，而且牠可以調節產下之卵數。寄主之體重和寄生蜂產下之卵數呈線性相關。若用人工加入額外的寄生蜂卵到寄主上，則寄生蜂之存活率，就隨著加入寄生蜂卵的多少而呈負相關的降低。雖然真正的產卵機制尚未清楚，但是麻痺寄主之注入毒液量並不能在決定產卵數之多少上提供資訊。雖然雌寄生蜂會按摩已麻痺的寄主，擠壓出其腸道中之內含物，提供後代免受污染的環境，但是寄生蜂並不具有照顧行為：例如把掉落在寄主體外之卵或幼蟲撿起並放回寄主體上。

關鍵詞：*Goniozus legneri*，產卵機制，外寄生蜂。

Introduction

Goniozus legneri Gordh is a gregarious ecto-parasitoid of the navel orangeworm (NOW), *Amyelois transitella* (Walker), which is the most serious pest in almond orchards of California (Gordh *et al.*, 1983). The parasitoid was imported into California from southern Uruguay for biological control of NOW (Legner, 1982a, b; Gordh *et al.*, 1983; Legner and Silverira-Guido, 1983). *G. legneri* has become widely established in almond orchards throughout California and significantly reduced the density of NOW (Legner and Warkentin, 1988). The parasitoid also appears promising for the control of pink bollworm, *Pectinophora gossypiella* (Saunders), in cotton fields of Arizona and California (Butler and Schmidt, 1985).

Several *Goniozus* species have been shown to be capable of regulating the number of eggs deposited on the host according to the size of the host (Gordh and Hawkins, 1981). My objective is to investigate what is the regulating mechanism in *G. legneri* and how it works. The maternal care of *G. legneri* is also investigated because several *Goniozus* species have shown some degree of maternal care (Chatterjee, 1941; Avasthy and Chaudhary, 1965; Gerling 1979).

Materials and Methods

Insects

The parasitoid, *G. legneri*, was obtained from laboratory culture in the Division of Biological Control, Department of Entomology, University of California, Berkeley. The adult parasitoids were kept in glass vials (4×0.5 cm diam.) with cotton plugs. Honey droplets were smeared on the wall of vials to supply food for the adults. Only 5-day-old female adults were used in the experiment. Larvae of the Mediterranean flour moth, *Anagasta kuehniella*, which came from a culture in the same laboratory, were used as substitute hosts and kept in plastic cups (6×6 cm diam.). Oatmeal was supplied as food source for the host.

Effect of host size on parasitoid oviposition and survival

Twenty hosts of different sizes were weighed and placed in an individual glass vial (4×0.5 cm diam.) with a 5-day-old mated female parasitoid. Honey was smeared on the wall as food for the parasitoid.

After 24 hours, the number of parasitoid eggs laid on the host was recorded, and females were dissected to determine the number of mature eggs remaining inside the bodies. This experiment was carried out at 27 ℃, with 12L: 12D conditions.

A similar experiment was set up except that the survival of the parasitoids was considered as an effect of the host size. The survivalship was calculated as: survivalship (%) =(number of adults emerged / total number of eggs laid) × 100.

Effect of extra eggs added on survival of the parasitoid

Forty *A. kuehniella* larvae were divided into four equal groups. Each larva was weighed before exposure to a female parasitoid. After 24 hours of ovipositional period, the female was removed and the number of eggs was recorded. The extra eggs of 0, 1, 2 or 3 of same age (within 6 hours), were added to each individual host of the groups immediately after removal of the female. The survivalship (%) of total parasitoid eggs on a host was calculated as an effect of extra eggs added. This experiment also was carried out at 27 ℃, with 12L: 12D conditions.

Measurement of host size by the parasitoid

Ten *A. kuehniella* larvae were weighed individually before exposing to a female parasitoid. As female parasitoids do not lay eggs until 20 hours after initial sting on the hosts (personal observation), each female was allowerd to paralyze a host but not oviposit. After 20 hours of exposure, each paralyzed host larva without any parasitoid egg on it was switched with another paralyzed larva. The females were allowed to oviposit on the switched hosts and the number of eggs laid were recorded. Based on the linear regression calculated from the host mass vs. number of parasitoid eggs in the experiment described in "Effect of host size on parasitoid oviposition and survival", the expected number of eggs laid according to the original or switched host mass was calculated. The x^2 test (Sokal and Rohlf, 1981) was employed to compare the number of eggs laid with the expected number of eggs on the original or switched host. The analysis was to determine which host provided the information for the parasitoid to decide the number of eggs to be laid.

Maternal care behavior of the parasitoid

As females were allowed to be with the hosts longer than the ovipositional period, females might respond to the sudden loss of eggs or larvae by laying more eggs. Twenty *A. kuehniella* larvae were set up for the oviposition of the parasitoid. After 24 hours, half the number of eggs laid were removed artificially from 10 hosts; then the parasitoids were kept with the same hosts in the vials. The remaining host larvae were kept for another 24 hours before half the number of parasitoid larvae were taken out. All female parasitoids were allowed to oviposit after artificial removal of eggs or larvae. The additional eggs laid and the development of larvae were observed.

In order to test whether *G. legneri* performs maternal care behavior to reposition disloadged eggs or larvae, twenty *A. kuehniella* larvae were used for the oviposition of the parasitoid. The experimental set-up was similar to the experiment described above, but only half the number of eggs of larvae was brushed off the hosts and placed in the vicinity of the hosts with the parasitoids. The fate of the brushed off eggs or larvae was recorded.

Results

Relationship between host body size and parasitoid eggs

The effect of host body size on the number of parasitoid eggs laid is shown

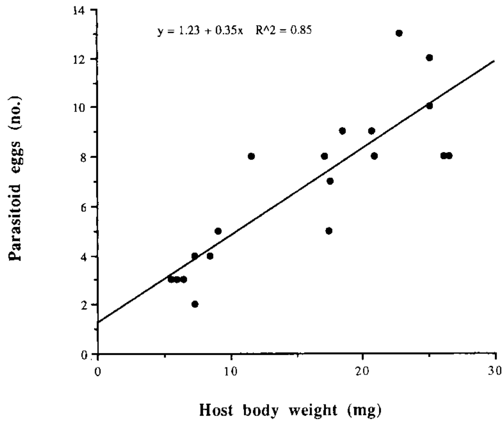

Fig. 1. Relationship between the mass of host, *Anagasta kuehniella*, and the number of eggs of parasitoid, *Goniozus legneri*, at 27 ℃, with 12L : 12D conditions (n=20).

in Fig. 1. It shows a positive relationship between body mass and number of eggs. The estimated linear regression is $y=1.23+0.35x$, in wlich y=no. of eggs, and x=body mass. The high correlation coefficient ($r^2=0.85$) indicates that the line represents the majority of the data. The mature eggs remaining in the female body after oviposition for 24 hours were 3.2 ± 0.9 (n=20). This result indicates that the parasitoid regulates the number of eggs laid on the host.

The body mass of the host showed no significant effect on the survival of the parasitoid (Fig. 2). This result indicates that the parasitoid utilizes the host tissue of any age, because host age is the main factor affecting the size in this experiment. The result also indicates that the number of eggs laid on hosts did not exceed the capacity of food supply for the parasitoid larvae.

The effect of extra eggs on the survival of the parasitoid is shown in Fig. 3 The addition of extra eggs definitely reduced the survival of parasitoid larvae, although developmental time for the surviving parasitoids from egg to adult was roughly the same in four treatments (11±1 days). The negative correlation between extra eggs and survival of parasitoids indicates that the original number of eggs laid on the host should be a maximum for that particular host.

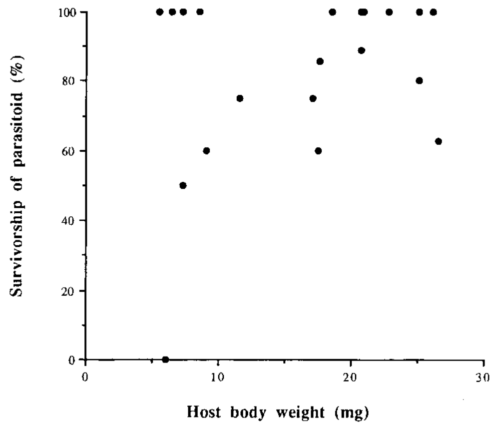

Fig. 2. Effect of body mass of *Anagasta kuehniella* on the survivalship of the parasitoid, *Goniozus legneri*, at 27 ℃, with 12L : 12D conditions (n=20).

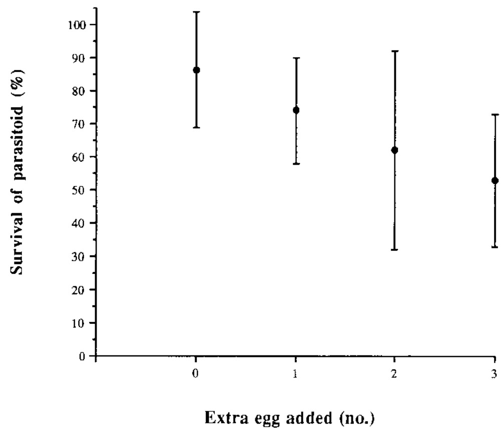

Fig. 3. Effect of addition of extra eggs on the survival of the parasitoid, *Goniozus legneri*, at 27 ℃, with 12L : 12D conditions (n=10).

Measuring host body size

The effect of host switching on the number of parasitoid eggs is shown in Fig. 4. The line, calculated from the data

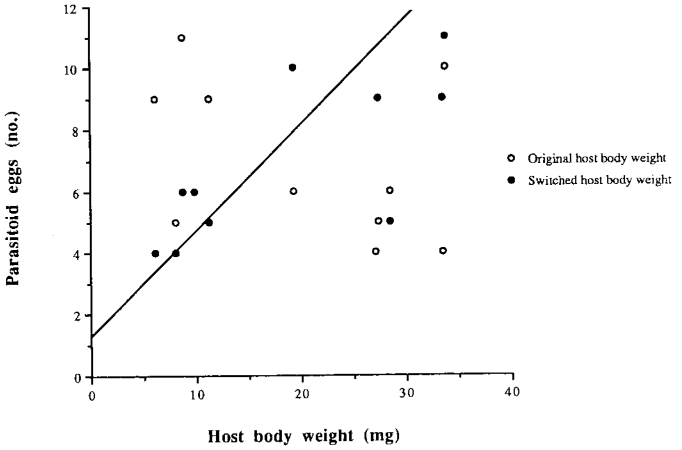

Fig. 4. Relationship between the number of eggs laid by the parasitoid, *Goniozus legneri* and body mass of host, *Anagasta kuehniella,* before and after switching hosts prior to oviposition (n=10). The line (y=1.23+0.35x) represents the relationship between host body mass and parasitoid eggs calculated from Fig. 1.

of Fig. 1, is the expected relationship between host mass and number of parasitoid eggs. The x^2 test for the original or switched groups to the expected line shows that actual number of eggs laid is based on the body mass of the switched host.

Maternal care behavior

All the females except three did not show continuous oviposition after half the number of eggs was removed. The survival of the remaining eggs, however, showed a slight increase from 83% to 91%. No female oviposited on a host that already had her larvae on it. The adult parasitoids never picked up the eggs or larvae which were artificially left in the vicinity of the hosts. All the eggs or larvae eventually died when left away from the host body.

Discussion

Although parasitoids in a high-density condition use the host tissues more efficiently than those in a low-density condition (Browne *et al.*, 1969; Lee and Chippendale, 1985), parasitoids tend to lay the number of eggs up to the host's capacity to support the development of larvae. According to the results (Fig. 1, 2 and 3), *G. legneri* actually regulated the maximum number of eggs laid on a host. The extra eggs added to the host reduced significantly the survival of the parasitoid. As the parasitoid completed development on diverse sizes of hosts (Fig. 2), the parasitoid was not restricted to attack a particular larval stage of the host. This finding also indicates that *G. legneri* has a desirable character as a biological control agent, because it can respond to the pest density more quickly in the field (Legner and Silveira-Guido, 1983).

There are several mechanisms that are likely to be counted to regulate the number of eggs laid on the host, such as visual sensory, walking distance, biting of mandibles, width of head capsule (Kishitani, 1961), sensory of oviposition, or volume of venom injected (Purrington and Uleman, 1972). It is possible that *G. legneri* may use all this information to decide how many offspring the host can support. However, the amount of venom injected to paralyze, but not to kill the host, enables more precise measurement of the size of the host. This relationship could be true for other ecto–parasitoids of which the ovipositors are the only body parts that can reach concealed hosts. Visual and body contacts of *G. legneri* with the host during oviposition and the close relationship between host body mass and the number of eggs laid (Fig. 1 and Fig. 4) seem to indicate that *G. legneri* utilizes other means than the volume of venom to measure the size of the host.

Because the larval development of *G. legneri* is rapid (about 3 days at 27 ℃), it would be beneficial for the species if all larvae on the same host developed synchronously. (Lee and Chippendale, 1985); the female should lay a clutch of eggs on a host a one time to prevent age variation among offspring on the same host. Therefore, it would make sense for the female not to lay eggs on the same host even with a few hours delay of oviposition. Three instances were observed in which females made up the lost eggs that were removed artificially. It is possible that the females were still in an ovipositing mode when half the number of eggs laid were removed, and no time gap between previous and present laid eggs was found. The pertinent finding of this experiment is that the female adults could sense the number of eggs existing on the hosts and oviposit to compensate the lost eggs.

Before depositing eggs on the paralyzed host, *G. legneri* used her mandibles to massage the host body in order to excrete gut contents. This behavior provides an environment relatively free of contamination for offspring, and also provides a means of measuring the size of a host, although the actual mechanism is unclear.

No host feeding was observed, in contrast to the finding of Gordh *et al.* (1983). As only one host was provided for one female during oviposition, host feeding might ruin the whole food source for her offspring. In addition, honey was a supplemental food source for adult females in all experiments; apparently females required no host feeding to mature eggs.

G. legneri used mandibles to bite an artificial intruder, such as forceps. However, the eggs or larvae that were left in the vicinity of the host were not picked up and replaced on to the host by females. This result indicates that *G. legneri* performs no elaborate maternal care behavior as biting off intruder might be the normal response of self defense. Doutt (1973) concluded that defending the potential host is evidently an adaptive feature to prevent hyper–parasitism and to increase the likelihood of immature survival. As the reasons for the larvae to leave the host in nature could be: (1) expulsion by the siblings, (2) shedding by the host, or (3) mandibles being not strong enough to clamp on the host, the separated larvae might represent unfit or weak individuals that should be eliminated according to natural selection.

Acknowledgments

I thank Dr. Leo Caltagirone for providing the experimental insects and for critically reading the earlier draft of this report, and Dr. S. B. Horng and two anonymous reviewers for their critical constructive suggestions.

References

Avasthy, P. N., and J. P. Chaudhary. 1966. Studies on *Parasierola* sp., a parasite of army worm. Ind. J. Entomol. 27: 414–422.

Browne, L. B., R. J. Bartell, and H. H. Shorey. 1969. Pheromone–mediated behavior leading to group oviposition in the blowfly *Lucilia cuprina*. J. Insect Physiol. 15: 1003–1014.

Butler, G. D. Jr., and K. M. Schmidt.

1985. *Goniozus legneri* (Hymenoptera: Bethylidae): development, oviposition, and longevity in relation to temperature. Ann. Entomol. Soc. Am. 78: 373–375.

Chatterjee, P. N. 1941. Notes on some parasites of shishan defoliators at Allahabad and Dehra Dun, India. Indian J. Entomol. 3: 157–172.

Doutt, R. L. 1972. Maternal care of immature progeny by parasitoids. Ann. Entomol. Soc. Am. 66: 486–487.

Gerling, D. J. 1979. *Parasierola*, a parasite of *Eldana saccharina* Wlk. Entomologist's Mon. Mag. 113: 211–212.

Gordh, G., and B. Hawkins. 1981. *Goniozus emigratus*, a primary external parasite of *Paramyelois transitella*, and comments on Bethylids attacking Lepidoptera. J. Kans. Entomol. Soc. 54: 787–803.

Gordh, G., J.B. Wooley, and R. A. Medved. 1983. Biological studies on *Goniozus legneri*, a primary external parasite of the Navel orange worm *Amyelois ransitella* and Pink bollworm *Pectinophora gossypiella*. Contrib. Amer. Entomol. Inst. 20: 433–468.

Kishitani, Y. 1961. Observations on the egg-laying habit of *Goniozus japonicus* Ashmead. Kontyu 29: 175–179.

Lee, H. J., and G. M. Chippendale. 1985. Development of *Iphiaulax kimballi* (Hymenoptera: Braconidae), and ectoparasite of the Southwestern corn borer, *Diatraea grandiosella* (Lepidoptera: Pyralidae). J. Kans. Entomol. Soc. 58: 509–516.

Legner, E. F. 1982a. New larvicidal wasp to attempt control of Navel orange worm. Almond Facts 47: 56–58.

Legner, E. F. 1982b. New wasp may help control Navel orange worm. Calif. Agric. 36: 4–6.

Legner, E. F., and A. Silveira-Guido. 1983. Establishment of *Goniozus emigratus* and *Goniozus legneri* (Hym: Bethylidae) on Navel orangeworm, *Amyelois transitella* (Lep: Phycitidae) in California and biological control potential. Entomophaga 28: 97–106.

Legner, E. F., and R. W. Warkentin. 1988. Parasitization of *Goniozus legneri* (Hymenoptera: Bethylidae) at increasing parasite and host, *Amyelois ransitella* (Lepidoptera: Phycitidae), densities. Ann. Entomol. Soc. Am. 81: 774–776.

Purrington, F. F., and J. S. Uleman. 1972. Brood size of the parasitic wasp *Hyssopus thymus*: functional correlation with the mass of a cryptic host. Ann. Entomol. Soc. Am. 65: 280–281.

Sokal, R. R., and J. Rohlf. 1981. Biometry. W. H. Freeman and Co., San Francisico, 859pp.

Received for publication July 14, 1992;
revised manuscript accepted August 6, 1992.