Bulletin of Entomological Research (2007) **97**, 185–190 doi:10.1017/S0007485307004841

Parasitism, development and adult longevity of the egg parasitoid *Telenomus nawai* (Hymenoptera: Scelionidae) on the eggs of *Spodoptera litura* (Lepidoptera: Noctuidae)

T. Fukuda[1], S. Wakamura[2]*, N. Arakaki[3] and K. Yamagishi[4]

[1]Kagoshima Prefectural Institute for Agricultural Development, 2200 Ohno, Kinpou-cho, Kagoshima, 899-3401, Japan: [2]Laboratory of Insect Behaviour, National Institute of Agrobiological Sciences, Ohwashi 1-2, Tsukuba 305-8634, Japan: [3]Okinawa Prefectural Agricultural Research Center, 820 Makabe, Itoman, Okinawa 901-0336, Japan: [4]Meijo University, Shiogamaguchi, Tempaku-ku, Nagoya 8502, Japan

Abstract

When *Telenomus nawai* Ashmead or *Trichogramma ostriniae* Pang & Chen (Hymenoptera: Trichogrammatidae) was inoculated into intact egg masses of *Spodoptera litura* (Fabricius) that were covered with a scale-hair layer, *T. nawai* emerged from 76% of the eggs, while emergence of *T. ostriniae* was from only 3% of the eggs. When the hair layer was removed before inoculation, the rate by the latter increased to 21%. These observations confirmed that the hair layer effectively protects *S. litura* egg masses from attack by *T. ostriniae*, and that *T. nawai* parasitism is more effective. In order to assess the feasibility of *T. nawai* as a biological control agent for *S. litura*, parasitism rate, development time and adult longevity were examined in the laboratory. Emergence of *T. nawai* was observed in more than 95% of 0- and 1-day-old separated eggs of *S. litura*, but the rate decreased to 60% and 0% for 2- and 3-day-old eggs, respectively. The emergence rates of *T. nawai* were near 95% for temperatures in a range from 25°C to 35°C, but decreased to 80% at 20°C. No parasitoids emerged at 15°C. The developmental periods decreased as temperature increased from 20°C to 35°C. The developmental threshold occurred at 13.7°C and 13.9°C, and the effective accumulative temperatures from egg to adult emergence were 149.3 and 147.1 degree-days for females and males, respectively. Mean longevity of the adult females decreased with increasing temperature; 87.0 days at 15°C and 9.5 days at 35°C. The feasibility of the use of *T. nawai* for controlling *S. litura* is discussed.

Keywords: parasitism, egg parasitoid, scale hair, development, longevity

Introduction

Spodoptera litura (Fabricius) is widespread throughout tropical and subtropical Asia and Pacific Islands. Larvae of *S. litura* feed on a variety of crop plants (Okamoto & Okada, 1968). *Spodoptera litura* inflicts serious attacks on soybean,

*Author for correspondence
Fax: +81 29 838 6205
E-mail: swaka@affrc.go.jp

sweet potato, taro and cabbage in Japan. The occurrence of this insect is sporadic and difficult to predict. Control has generally relied on chemical pesticides. Insecticides are effective against young larvae but some fail to control grown larvae or have become ineffective after the development of larval resistance (Hirose, 1995).

Usually *S. litura* does not survive winter in outdoor conditions except in a limited area of southwestern Japan (Naito, 1987; Matsuura *et al*., 1991; Matsuura & Naito, 1997). The *S. litura* populations that are present in the early season may also originate from populations that overwinter in greenhouses and disperse northwards every year in Japan (Naito, 1987). Populations may also contain migrants from overseas (Murata *et al*., 1998). The density increase of this insect is gradual from spring to early summer and then accelerates from mid-summer to autumn in southwestern Japan (Wakamura *et al*., 1992). Severe damage is frequent. Life table research suggested that outbreaks of *S. litura* may be induced by the reduction of natural pressures from natural enemies, which include the egg parasitoid, *Telenomus* sp. (Yamanaka *et al*., 1972).

The efficiency of egg parasitoids as control agents against lepidopterous pests is widely recognized (Wajnberg & Hassan, 1994). In a preliminary survey conducted in a cabbage field of Ibusuki, Kagoshima, Japan in 2001, the author (T.F.) and co-workers found that *Trichogramma* sp. (Hymenoptera: Trichogrammatidae) emerged from more than 40% of *S. litura* egg masses but from less than 10% of the eggs within those egg masses. This suggested that *Trichogramma* is not very effective in controlling *S. litura*. We found another egg parasitoid, *Telenomus nawai* Ashmead, on *S. litura* egg masses in taro fields at Tsukuba, Japan in 2002. This parasitoid has been known as an egg parasitoid of *Spodoptera depravata* (Butler) (Arakaki *et al*., 2000). *Telenomus nawai* is considered an important natural enemy of the *Spodoptera* moths in Japan (Arakaki *et al*., 2000), but information about this wasp is limited.

In general, eggs that are left without any protection and are exposed to natural enemies will not persist. Various types of materials are used for protection (Gross, 1993). Egg masses of *S. litura* are usually covered with scale-hair, which protect them from a generalist parasitoid *Trichogramma chilonis* Ishii (Ohta *et al*., 1994). We found that *T. nawai* emerged from many eggs of *S. litura* egg masses despite this protective layer of scale-hair.

In this paper, we report the effective parasitism on egg masses of *Spodoptera litura* by *Telenomus nawai* in comparison with that by *Trichogramma ostriniae* Pang & Chen, which was collected at Ibusuki and successively reared in the laboratory of the KPIAD as a possible control agent for various lepidopterous pests including *S. litura*. Developmental time and adult longevity of the parasitoid at five constant temperatures in the laboratory was also investigated. This provides fundamental information for assessment of the feasibility of *T. nawai* as a biological control agent of *S. litura*.

Materials and methods

Insects

Spodoptera litura larvae were collected from a wild population that fed on the leaves of cabbage, *Brassica oleracea* L., in Ibusuki, Kagoshima Prefecture, in late May 2002. Larvae were successively reared in the laboratory and fed an artificial diet (Insecta LFS, Nihon Nousan Kogyo Co., Yokohama) in a plastic case (30 cm long × 23 cm wide × 8.5 cm high, *c*. 20 larvae per case) at 25°C and 14L : 10D until pupation. Pupae were removed from the rearing case and kept in glass cylinders (9 cm internal diameter × 6 cm high, *c*. 5 pupae per cylinder) until emergence. Two pairs of females and males of *S. litura* were confined in another glass cylinder, the inside walls of which were covered with a filter paper (6 cm × 30 cm, Toyo No. 2). They were provided with a small piece of absorbent cotton that had been immersed in 5% honey solution. Egg masses laid on the paper were removed by cutting the paper around them with scissors. Hatching rate of the eggs was generally more than 99% in the laboratory culture.

Telenomus nawai were obtained from *S. litura* egg masses laid on taro leaves at Tsukuba in early September 2002. They were successively reared on *S. litura* egg masses at 25°C and 14L : 10D. Males emerged slightly earlier than females, waited for female emergence on the egg mass, and mated immediately when a female emerged. For the experiments, mated females and males were used. Adult wasps were kept in a glass tube (15 mm internal diameter × 18 cm long) at 15°C and 14L : 10D until use in experiments. They were fed honey that was streaked on the tube wall.

Trichogramma ostriniae used in this experiment were provided by Dr H. Inoue of the Kagoshima Prefectural Sericultural Experiment Station (currently, KPIAD). The laboratory culture originated from individuals that had emerged from *Plutella xylostella* (Linnaeus) (Lepidoptera: Yponomeutidae) eggs collected in cabbage fields at Ibusuki, Kagoshima, in October 1994, and was successively maintained on *Ephestia kuehniella* (Zeller) (Lepidoptera: Pyralidae) eggs. In the present study, *T. ostriniae* were kept on the *S. litura* eggs for more than three generations. Egg masses or isolated eggs of *S. litura* were provided to *T. ostriniae* after most scale-hair that covered the egg masses was removed to expose the eggs. Scale-hair was removed by scrubbing the surface of intact egg masses with a fine soft brush. *Trichogramma ostriniae* adults emerged from 50–60% of the eggs of those egg masses. Mated females were used for the experiments.

Emergence of T. nawai *and* T. ostriniae *from* S. litura *egg masses*

Single egg masses of *S. litura* collected within 12 h after oviposition were mounted on filter paper sheets (*c*. 1.2 cm × 3 cm) and offered to two female adults of *T. nawai* in a glass tube (15 mm internal diameter × 18 cm long). Mean number of eggs per egg mass was 328 (range 219–542). The tubes were plugged with a silicon sponge (Silicosen®, Shin-Etsu Polymer Co., Ltd, Tokyo), and kept at 25°C and 14L : 10D. The parasitoids were removed 24 h after the introduction. A *S. litura* egg mass with or without scale-hair layer was also presented to two *T. ostriniae* females in the glass tube. The egg masses were otherwise kept in their initial condition, and emerged parasitoids and/or hatched larvae of *S. litura* were counted and removed every day until the emergence or hatching ceased. Treatments had five replications. Hatching rates (X) of *S. litura* were transformed to $\arcsin(X^{1/2})$ and submitted to one-way-layout ANOVA and subsequent Tukey's ranking.

Table 1. Effect of age of *Spodoptera litura* eggs on emergence rate (%) of *Telenomus nawai* ($n = 60$).

Host age (days)	Emergence of *T. nawai*[a]	Hatching of *S. litura*[a]	Egg mortality
0	97 a	0 c	3
1	100 a	0 c	0
2	60 b	33 b	7
3	0 c	100 a	0

[a] Values accompanied with the different letters in the same column are significantly different by 4 × 2 chi-square test and subsequent paired chi-square test ($P < 0.001$).

Optimum host age for T. nawai

To determine the optimum host age for the parasitoid, 0-day-old *S. litura* eggs were separated from egg masses after the scale-hair was removed. Twenty eggs were pasted on a paper sheet (1.2 cm × 3 cm) with water-soluble glue. The paper sheet with eggs was placed in a glass tube and single 1-day-old *T. nawai* females were introduced on day 0, 1, 2 or 3. The tubes were plugged and kept at 25°C and 14L : 10D. The parasitoids were removed 24 h after introduction. Eggs were then kept under the same conditions, and the emergence of parasitoids and/or hatching of *S. litura* larvae were checked every day. Treatments were replicated three times and the data were pooled for the three replications. For the comparisons of rate values, when the 4 × 2 chi-square test was significant, paired chi-square test at Bonferroni's corrected *P* value were subsequently applied. The values accompanied with the same letter in table 1 are not significantly different at the $P = 0.05$ level.

Effect of temperature on development of T. nawai

Twenty separated and naked 0-day-old *S. litura* eggs were pasted on a paper sheet (1.2 cm × 3 cm) and placed together with a single 1-day-old *T. nawai* female in a glass tube. The parasitoids and host eggs were kept at 25°C for 24 h, and then the parasitoids were removed. The exposed eggs were held in the tube at a constant temperature of 15°C, 20°C, 25°C, 30°C or 35°C and 14L : 10D. The emergence of parasitoids and/or *S. litura* larvae was checked every day. The treatments had three replications and subsequently each of the 60 eggs were examined for each temperature.

Adult longevity of T. nawai

To evaluate longevity of the parasitoid adults in the absence of hosts, 15 female and male parasitoids were individually held in glass tubes at a constant temperature of 15°C, 20°C, 25°C, 30°C or 35°C and 14L : 10D. They were provided with undiluted honey streaked on the tube wall. Mortality was checked every day.

Results

Emergence of T. nawai *from* S. litura *egg masses*

When intact egg masses of *S. litura* were exposed to *T. nawai* females (day 0), *S. litura* larvae hatched from only 2.3% of the eggs in the egg masses on day 4 and the parasitoids emerged from 75.5% of the egg masses on days 12–14. The remaining 22.2% of the eggs were broken

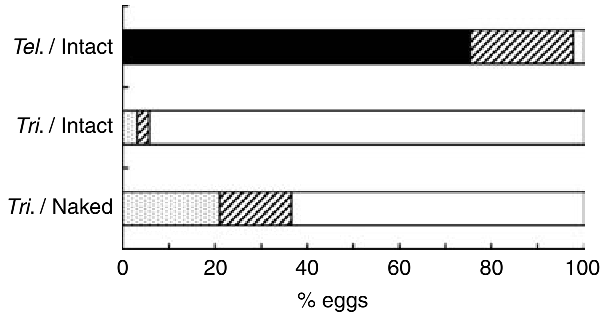

Fig. 1. Parasitism of eggs in intact and naked egg masses of *Spodoptera litura* by *Telenomus nawai* (*Tel.*) and *Trichogramma ostriniae* (*Tri.*) ($n = 5$). Means of the hatching rates of the host eggs were significantly different between *Tel.*/Intact and *Tri.*/Naked, and *Tri.*/Naked and *Tri.*/Intact ($P < 0.01$). Egg mass size; *Tel.*/Intact: 230, 273, 280, 376, and 382, *Tri.*/Intact: 219, 258, 385, 519 and 542, *Tri.*/Naked: 258, 260, 296, 323, and 326 (■, *Tel.*; ▨, *Tri.*; ▨, Dead; □, *Spodoptera*).

(fig. 1, *Tel.*/Intact). In those egg masses, host larvae were observed to hatch from the lower layer of the egg masses earlier than the parasitoids. After the host larvae emerged, broken eggs were observed around the exit holes in the upper layers of the egg masses. We considered these eggs to have been parasitized by *T. nawai*, although they had also been broken by feeding and/or crawling by the host larvae.

Telenomus nawai female adults were observed to crawl into the hair layer to parasitize eggs of *S. litura*. The hair layers of all the egg masses from which *T. nawai* emerged were disturbed by the parasitoids. In contrast, when an intact egg mass was exposed to *T. ostriniae* females on day 0, the offspring parasitoid emerged from only 2.9% of eggs in the egg masses on days 9–11 (fig. 1, *Tri.*/Intact) and the rate increased only to 21%, even when the hair layer had been removed (*Tri.*/Naked). The means of the hatching rates of the host eggs were significantly different between *Tel.*/Intact and *Tri.*/Naked, and *Tri.*/Naked and *Tri.*/Intact ($P < 0.01$).

Optimum host age for T. nawai

Emergence of *T. nawai* was observed in 97–100% of 0- to 1-day-old host eggs. The rate significantly decreased to 60% for 2-day-old eggs, and the 3-day-old eggs yielded no parasitoids and gave rise to *S. litura* hatchings (table 1). Emergence rates were significantly different between 0-day or 1-day-old and 2-day-old eggs and 2-day-old and 3-day-old eggs. Hatching rates of *S. litura* eggs were 33% and 100% for 2- and 3-day-old eggs, respectively.

Effect of temperature on development of T. nawai

Table 2 shows the emergence rates and the developmental periods from egg to adult in *T. nawai*. Adult emergence occurred at all temperatures tested except for 15°C. The rates of adult emergence were 95% for a temperature range from 25°C to 35°C, and 80% at 20°C. No wasps emerged at 15°C during the 5-month observation period; all the eggs collapsed or mildewed and died.

Developmental periods decreased as temperature increased from 20°C to 35°C (table 2). The regressions of developmental rate (Y d^{-1}) on temperature (X °C) from egg

https://doi.org/10.1017/S0007485307004841 Published online by Cambridge University Press

Table 2. Emergence rates and developmental periods of *Telenomus nawai* on *Spodoptera litura* eggs at five constant temperatures.

Temperature (°C)	Emergence rate (%)[a]	Developmental periods (days, mean ± SD)[b]	
		Female	Male
15	0	–[c]	–[c]
20	80	26.4 ± 1.1 (33)	25.6 ± 0.8 (15)
25	95	13.0 ± 0.2 (35)	12.7 ± 0.5 (22)
30	95	9.0 ± 0.2 (35)	9.0 ± 0.0 (22)
35	95	7.0 ± 0.2 (35)	7.0 ± 0.0 (22)

Regressions of developmental rate (Y d^{-1}) on temperature (X°C) were: $Y = 0.067X - 0.0915$ ($r^2 = 0.996$) for females and $Y = 0.068X - 0.0943$ ($r^2 = 0.998$) for males.
[a] Sixty *S. litura* eggs were used at each temperature.
[b] Values in parentheses show the numbers of emerged parasitoids.
[c] No insect emergence.

to adult emergence were significant at the $P = 0.001$ level in both sexes; female: $Y = 0.0067X - 0.0915$ ($r^2 = 0.996$), male: $Y = 0.0068X - 0.0943$ ($r^2 = 0.998$). The lower development threshold for the females and males occurred at 13.7°C and 13.9°C, and effective accumulative temperature from egg to adult emergence for females and males were 149.3 and 147.1 degree-days, respectively. The developmental period was not significantly different between sexes at all temperatures tested, while males were observed to emerge earlier than females to wait for female emergence on the egg masses.

Adult longevity

Adult longevity of *T. nawai* was significantly increased at lower temperatures in both sexes (table 3). The regressions of reciprocals of longevity (Y d^{-1}) on temperature (X°C) were $Y = 0.00469X - 0.0670$ ($r^2 = 0.935$, $P < 0.01$) for females and $Y = 0.0132X - 0.227$ ($r^2 = 0.733$, $P = 0.064$) for males. In males, the value at 35°C was much shorter than that in females. When this value was excluded, the regression became significant: $Y = 0.00530X - 0.0695$ ($r^2 = 0.921$, $P = 0.040$). Females lived significantly longer than males at temperatures of 15, 20 and 35°C.

Discussion

We collected *T. nawai* from the *S. litura* egg masses laid on taro leaves in Tsukuba, Japan. This is probably the first record of *T. nawai* as an egg parasitoid of *S. litura*, although it has been collected from egg masses of *S. depravata* in Tsukuba (Arakaki *et al*., 2000). Arakaki *et al*. (2000) also collected *Telenomus* sp. from *S. litura* egg masses in Okinawa. This parasitoid was thelytokous, but seemed to be a conspecific population of *T. nawai* infected by *Wolbachia* (Arakaki *et al*., 2000). Yamanaka *et al*. (1972) found high parasitism of *S. litura* egg masses on taro leaves by *Telenomus* sp., and Hamada (1992) obtained one species of *Telenomus* from *S. litura* egg masses on taro and soybean leaves in the fields at Tsukuba, Ibaraki, between August and September, 1984. No further species identification or investigations have been conducted by these authors.

Telenomus nawai emerged from 76% of host eggs in the intact egg masses covered with scale-hair. The mean hatching rate of *S. litura* eggs was greatly reduced to 3% (fig. 1). This suggests the high potential of *T. nawai* as a control agent of *S. litura* population in the field. In contrast, *T. ostriniae* emerged from only 3% of host eggs in the intact egg masses. This rate increased for *T. ostriniae* to 21% when most of the scale-hair had been removed from the egg masses to expose the eggs (fig. 1). This rate was considerably lower than the values for the same species in our successive rearing (55–60%, T. Fukuda, unpublished data) in which *S. litura* eggs were completely separated from the egg masses and scale-hair. Residual scale-hair on the egg masses probably disturbed oviposition of *T. ostriniae* in the above experiment.

The differences between *T. nawai* and *T. ostriniae* in parasitism of intact egg masses may be due to differences in oviposition behaviour. We observed that *T. nawai* crept into the hair layer covering the *S. litura* egg masses, while *T. ostriniae* did not. A congeneric species, *Telenomus euproctidis* Wilcox, was also found to creep into the dense hair layer of *Euproctis taiwana* (Shiraki) (Lepidoptera: Lymantriidae) egg masses (Arakaki, 1990). Hamada (1992) recorded, *Trichogramma dendrolimi* Matsumura, *T. chilonis*, *Trichogramma* sp. and *Telenomus* sp. as egg parasitoids of *S. litura* in Tsukuba, Japan. However, *T. chilonis* seldom attacked *S. litura* egg masses covered with a hair layer (Ohta *et al*., 1994). As noted in the present paper, this was also true for *T. ostriniae*. This appears to be the reason why *Trichogramma* sp. parasitized less than 10% of the eggs in *S. litura* egg masses in the field (T. Fukuda, unpublished data).

The emergence rate of *T. nawai* from the intact egg masses of *S. litura*, shown in fig. 1, was lower than that expected from the isolated and naked eggs in table 1. At least two explanations for this are possible. Firstly, *S. litura* larvae hatch from the eggs within four days at 25°C (Miyashita, 1971), but *T. nawai* require a longer time to complete the development on *S. litura* eggs at the same temperature (table 2). Therefore, host larvae that hatched might have fed on eggs parasitized by *T. nawai*, resulting in a decrease of emergence of the parasitoids. Secondly, *S. litura* females usually lay egg masses with two or three layers, and thus the eggs on the lower layers can escape from attack by *T. nawai*. Layered egg masses have been also found in the peacock

Table 3. Mean adult longevity (d) of *Telenomus nawai* at five constant temperatures ($n = 15$).

Temperature (°C)	Females		Males		*t*-test
	Mean ± SD	Range	Mean ± SD	Range	
15	87.0 ± 19.7	52–120	69.1 ± 16.4	51–112	$P < 0.01$
20	61.8 ± 27.4	7–110	41.1 ± 15.6	18–66	$P < 0.05$
25	18.2 ± 7.5	2–27	13.5 ± 6.4	2–24	$P > 0.05$
30	15.9 ± 3.8	7–20	11.6 ± 4.2	2–18	$P > 0.05$
35	9.5 ± 4.9	1–14	3.2 ± 2.2	0–8	$P < 0.05$

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butterfly, *Inachis io geisha* (Stichel) (Lepidoptera: Nymphalidae) (Hondô *et al*., 1995) and the gypsy moth, *Lymantria dispar* (Linnaeus) (Lepidoptera: Lymantriidae) (Hitchcock, 1959). These females are considered to stack their eggs to guard the lower layers from parasitoids.

Maximum mid-summer temperatures in southwestern Japan exceed 30°C, and the field density of *S. litura* increases rapidly from mid-summer to autumn. This population increase is probably caused by an escape from natural enemies in this season as Yamanaka *et al*. (1972) suggested. Adult emergence of *T. nawai* was 95% at 30°C and 35°C (table 2), indicating that high temperature has little influence on the emergence of *T. nawai*. This heat hardiness may be adaptive in the high temperature zones of south-western Japan. However, *S. litura* eggs hatched within three days at temperatures of 30°C and 35°C (Miyashita, 1971), and were susceptible to parasitism by *T. nawai* for only two days after oviposition even at 25°C (table 1). This means that the effectiveness of *T. nawai* as a biological control agent against *S. litura* is limited to within only one or two days after the oviposition by the host. Successive mass releases of this parasitoid may be necessary for successful control of *S. litura*. Males have a short adult span at a higher temperature of 35°C (table 3), but this may not affect reproduction since we observed in our experiment that males emerged as adults earlier than females and then waited for females to copulate soon after emergence. Early emergence of males has also been observed in several *Telenomus* species (Schwarts & Gerling, 1974; Chabi Olaye *et al*., 1997; Fantinou *et al*., 1998).

Adult females of *Telenomus alsophilae* Viereck and *Telenomus californicus* Ashmead are known to survive for four months or more (Fedde *et al*., 1979; temperature data were not presented). Such long-lived species of *Trichogramma* are not known. Adults of *Telenomus busseolae* Gahan survive up to 12 weeks at 8 and 12°C (Bayram *et al*., 2005). In the present study, the longevity of *T. nawai* females was significantly prolonged as temperature decreased, while the regression for this effect was marginally significant in males (table 3). The longer adult span of *T. nawai* females at lower temperature (>2 months at 20°C and 15°C; table 3) indicates that long-term preservation of this species is possible for long periods. If techniques of mass production and low temperature management of *T. nawai* are established, this species could serve as a powerful biological control agent of *S. litura*. The effectiveness of *T. nawai* against the field population of *S. litura* should be a subject of future research.

Acknowledgements

This research was mainly accomplished during the work of Takeshi Fukuda with the Laboratory of Insect Behaviour, NIAS. The authors sincerely thank V.N. Fursov for identification of *T. ostriniae*, and Seiji Tanaka and Toshiharu Akino of NIAS for critical reading of the manuscript. The authors also thank Tetsuya Yasuda, Toshiharu Akino, Hiroe Yasui and Midori Fukaya of the NIAS laboratory for their helpful discussions and encouragement. Thanks are also due to Tatsuro Muta, Takuhiro Yamaguchi and the other staff of the Kagoshima Prefectural Experiment Station, who gave Takeshi Fukuda a leave opportunity to work at NIAS, and encouragement throughout this study.

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(Accepted 23 October 2006)