Biological parameters of the egg parasitoid *Trissolcus grandis* (Hym.: Scelionidae) on *Eurygaster integriceps* (Hem.: Scutelleridae)

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Abstract

Trissolcus grandis Thomson is a solitary egg parasitoid of Sunn pest, *Eurygaster integriceps* Puton. Although widely distributed, it has often been overlooked in field surveys. Our objectives were to develop an efficient rearing technique for *T. grandis*, and to determine the basic bionomics and demographic parameters, necessary for future augmentative biological control programs. Exposure of 0-4 h-old Sunn pest egg masses to parasitoids at 1:1, 2:1 and 3:1 host-parasitoid ratios resulted in a parasitism rate of > 80%. The results demonstrated that the age of the host and the exposure time affected parasitism rate. However, parasitism rate did not differ significantly among 24, 48 and 72 h-old Sunn pest eggs. The percent of emerged parasitoids during the 24-h host exposure period was relatively high when host eggs were 24 h old. Moreover, the mean sex ratio showed a definite trend, suggesting that host age had an effect on the sex ratio of the *T. grandis* offspring. The mean developmental time obtained as 11.091 ± 0.1 and 9.68 ± 0.15 d. for female and male progenies, respectively. The longevity of females was ~ 30% lower compared to that of males. The average net fecundity reached 181.83 eggs per female. On the other hand, a female laid averagely ~ 7 eggs per day. Similarly, the daily population increase and mean generation time were 34.2%, and 14.61 d, respectively. The developing population consisted of 99% immature (egg, larvae, pupa), and only 1% adults. The importance of these findings to the population biology of this parasitoid is discussed.

Key words: *Trissolcus grandis*, biological control, demographics, *Eurygaster integriceps*

چکیده

زنبور *Trissolcus grandis* Thomson، مهم‌ترین پارازیتویید انفـرادی تخـم سـن گنـدم، *Eurygaster integriceps* Puton، است. بااین‌که این حشره دارای پراکنش وسیعی در ایران می‌باشد، اما غالباً نقش آن نادیده گرفته شده است. هدف از این بررسی تعیین ویژگی‌های زیستی و بهینه‌سازی روش پرورش این پارازیتویید به‌منظور کـاربرد آن در برنامـه‌هـای کنتـرل بیولوژیک سن گندم بود. میزان پارازیتیسم زمانی‌که نسبت میزبان- پارازیتویید ۱:۱، ۲:۱ و ۳:۱ بود، به بیش از ۸۰ درصد رسید. اگرچه بین سنین ۲٤، ٤۸ و ۷۲ ساعت میزبان تفاوت معنی‌داری وجود نداشت، سن میزبان و مـدت زمـان آرایـه‌ی آن، روی میزان پارازیتیسم مؤثر بود. بالاترین میزان درصد خروج زمانی‌که دسته‌های تخم ۲٤ ساعته به مدت ۲٤ ساعت در اختیار زنبور پارازیتویید قرار گرفت، مشاهده شد. علاوه بر این، سن میزبان بر میانگین نسبت جنسی نتاج پارازیتویید نیز مؤثر بود. متوسط طول دوره‌ی رشدی ماده‌ها و نرها به ترتیب ۰/۱۵ ± ۱۱/۰۹۱ و ۰/۱ ± ۹/٦۸ روز بود. نتایج نشان داد طول عمر ماده‌ها حدود ۳۰ درصد کمتر از نرها است. متوسط باروری خالص ۱۸۱/۸۳ تخم و متوسط نرخ روزانه‌ی تخم‌ریزی حدود ۷ تخم در روز به دست آمد. افزایش روزانه‌ی جمعیت ۳٤/۲ درصد و متوسط مدت زمان یک نسل ۱٤/٦۱ روز بود. در چنین حالتی، ۹۹ درصد از جمعیت را مراحل نابالغ (تخم، لارو و شفیره) و فقط ۱ درصد از جمعیت را حشرات بالغ تشکیل می‌داد. اهمیت این یافته‌ها در زمینه‌ی بیولوژی جمعیت این پارازیتویید مورد بحث قرار گرفته است.

واژگان کلیدی: *Trissolcus grandis*، کنترل بیولوژیک، دموگرافی، *Eurygaster integriceps*

Introduction

Wheat is a staple crop and has the first rank of cultivated crop in the world. There are about 6.4 million ha irrigated and rain-fed land under wheat in Iran. One of the critical limitations to the quality crop harvest is Sunn pest, *Eurygaster integriceps* Puton, an important pest of wheat and barley throughout west and central Asia. It has caused major concern for more than 70 years (Critchely, 1998). Overwintering for about 8 months a year, the univoltine pest migrates from mountains to the nearby fields in the spring and starts its new generation each year. About 70 years back, its biological control continued for almost 2 decades by use of scelionid egg parasitoids as the first augmentation practices in Iran but it ceased for unknown reasons (Safavi, personal communication). Since then, unfortunately, the chemical control of Sunn pest became the only pest control strategy so that about 1 million ha of wheat has been sprayed with pesticides in recent years, annually (Anonymous, 2007). However, with the growing concerns on the health and environmental hazards caused by the conventional use of insecticides, there has been a renewed and encouraging approach in biological control of Sunn pest (Amir-Maafi, 2000). There are a number of natural enemies attacking Sunn pest, among which, scelionid wasps are of great importance (Safavi, 1968).

The scelionid wasp, *Trissolcus grandis* Thomson, has shown considerable promise in its ability to regulate Sunn pest populations (Amir-Maafi, 2000; Amir-Maafi & Parker, 2002, 2003). Different studies have been conducted on the biology and rearing methods of *T. grandis* (Safavi, 1968; Shapiro *et al.*, 1975, Gusev & Shmettser, 1977; Taghadosi, 1991; Shahrokhi, 1997; Amir-Maafi, 2000; Shirazi, 2006). Nowadays, an integrated management strategy is being developed for *E. integriceps* based on utilization of a complex of hymenopteran egg parasitoids which suppress Sunn pest populations during the spring (Amir-Maafi, 2000). The dominant species in this complex is *T. grandis*. This species comprised 70% of parasitoids collected from *E. integriceps* eggs from 2000-2007 in Iran.

The objectives of this study were: (1) developing an efficient mass rearing technique for *T. grandis*; (2) estimating basic demographic parameters that could be used in future ecological and biological control researches.

Materials and methods

Insect colonies

Sunn pest parasitized egg masses were collected from wheat and barley fields in Varamin, Iran, during April to May, 2007. Emerged wasps were identified and laboratory cultures of *T. grandis* were established in ventilated polystyrene boxes (20 × 14 × 7 cm [l × w × d]). A very minute quantity of honey on a piece of paper card (1 × 10 cm) was placed in each box to provide food for adults. Moreover, a plastic tube, 2.5 cm diameter and 10 cm length, containing water and clogged with cotton wool was installed on the boxes through a central hole as water reservoir. Food and water were renewed every week. Cultures were kept at 16 ± 1 ºC, 65 ± 5% RH and 8: 16 (L: D) h photoperiod. Parasitoids could be maintained in the laboratory under these conditions for several months.

In January 2008, approximately 2000 pairs of Sunn pest were collected from an overwintering site in Gharah-Aghaj mountain, located at 30 km north of Varamin and were used to start a laboratory culture. The insects were sexed and about 100 to 250 pairs were kept in plexiglas cages (60 × 38 × 30 cm [l × w × d]) at 25 ± 0.5 ºC, 65 ± 5% RH., and 16: 8 (L: D) photoperiod. They were also provided with water and wheat grains (Mahdavi variety). A number of paper strips (60 × 1 cm) were hanged from a metal frame on the top of the cages as substrates for oviposition. Egg masses were collected daily by removing paper strips and cutting them into pieces containing one egg mass. Each egg mass contained approximately14 eggs and was used in experiments (< 4 hours old) or kept for colony rearing.

One hundred *T. grandis* females were transferred individually into glass tubes and provided with one fresh egg mass of Sunn pest. Then, they were kept for 2 d at 25 ± 0.5 ºC, 65 ± 5% RH and 16: 8 (L: D) h photoperiod. Newly emerged adult parasitoids (F_1) were used for experiments.

The experiments were conducted in polystyrene boxes measuring 14l × 7w × 4d cm. There was a 2.5 cm Ø hole covered with fine-mesh muslin cloth on two sides of each box for ventilation. Besides, three holes were made on the lid, one with 2.5 cm Ø in the center and two with 1.5 cm Ø on either side of the central one. A plastic tube (10 × 2.5 cm) containing water and plugged with cotton wool, was inserted in the central lid hole. The other two holes on the lid were used to introduce or to remove the parasitoids and egg masses, or for providing honey. When not in use, they were sealed with a cork stopper. Food and water were renewed daily. Host eggs were provided by gluing the pieces of paper strips that contained Sunn pest egg masses on a white index card (1 × 10 cm). All tests described below were done under these conditions.

Host-parasitoid ratios

To determine the optimal ratio of Sunn pest egg masses to parasitoid density in mass rearing conditions, six *T. grandis* females (one d old and mated and without previous oviposition experience) were placed individually into an a.m. experimental cages, already containing 1, 2, 3, 4, 5 or 10, 0-4 h-old Sunn pest egg masses. Therefore, six host:parasitoid ratios of 1:1, 2:1, 3:1, 4:1 5:1 and 10:1, replicated 8 times, resulted in 48 experimental units. The cages were kept in a rearing room at 25 ± 0.5 ºC, 65 ± 5% RH and 16: 8 (L: D) photoperiod. After 24 h, egg masses were removed from cages and kept separately in tubes at the mentioned room conditions for 3 wks to allow progeny emergence.

Host age and exposure time

To determine the optimal host age and duration of exposure to parasitoids, treatments of 24-, 48-, 72- and 96-h-old Sunn pest egg masses were used, each exposing for 1, 4, 8 and 24 h. Two egg masses (28 eggs) were exposed to 1 parasitoid in each test replicated 10 times at 25 ± 0.5 ºC, 65 ± 5% RH and 16: 8 (L: D) photoperiod. At the end of each exposure time, egg masses were transferred to tubes and maintained at the same conditions for 3 wks to allow for emergence of *T. grandis*.

Development time

Developmental times for immature *T. grandis* were recorded by exposing 20 1-d old Sunn pest egg masses (280 eggs) to *T. grandis* females for 4 h at 25 ± 0.5 ºC, 65 ± 5% RH and 16: 8 (L: D) photoperiod. Afterwards, the egg masses were observed daily at the same conditions until all parasitoids completed emergence. The developmental duration of male and female progenies was recorded in days.

Life table parameters

Twenty five randomly chosen and newly emerged females (< 24 h-old and mated) of *T.* grandis were transferred individually to the experimental cages. Each female parasitoid was presented 2 Sunn pest egg masses (28 eggs) and honey as food at 25 ± 0.5 ºC, 65 ± 5% RH and 16: 8 (L: D) photoperiod. The egg masses and honey were changed daily until the female died. The parasitized eggs were incubated for three wks at the same conditions till the emergence of *T. grandis*. The number of parasitized eggs (fecundity), sex ratio of progeny, percent emergence and survival of parent wasps were recorded per day.

Statistical analyses

Means and standard errors were calculated for percentage parasitism, percentage parasitoid emergence and sex ratio (♂/♀ + ♂). The General Linear Models analysis of variance (PROC GLM; SAS Institute, 1987) was used to determine the effects of host:parasitoid ratio, host age and exposure time on parasitism, emergence rate and sex ratio. All percentage data were arcsine transformed (square root of the proportion) before analysis. The Duncan's Multiple Range Test was used to separate differences between transformed means ($P = 0.05$; SAS Institute, 1987). Population parameters, life and fertility tables were estimated following the methods described in Carey (1993).

Results

Host ratio and egg ages

The ratio of host to parasitoid influenced significantly parasitism rate ($F = 8.80$; df = 5, 42; $P = 0.0001$). Parasitism was highest using a ratio of 1:1, 2:1 and 3:1 (host:parasitoid) (fig. 1). Age of host also affected parasitism rate ($F = 6.25$; df = 3, 153; $P = 0.0005$) as well as host exposure time to parasitoid ($F = 30.34$; df = 3, 153; $P = 0.0001$). Ninety six-h-old eggs were the least parasitized at any exposure time (fig. 2). Parasitism rates did not differ between 24, 48 and 72-h-old.

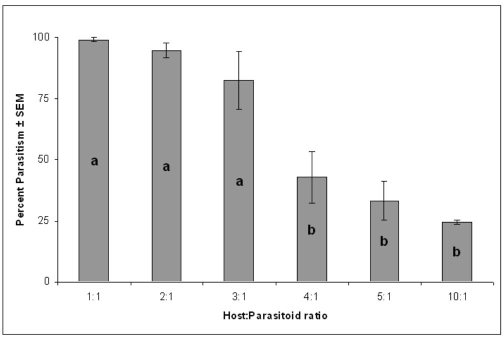

Figure 1. Effect of host-parasitoid ratio on *T. grandis* parasitism (mean ± SE) of Sunn pest egg masses at 25 ± 0.5 ºC, 65 ± 5% RH and 16: 8 (L: D) photoperiod. Bars with the same letters are not significantly different at α = 0.05.

The percent of emerged parasitoids during the 24-h host exposure period was relatively high when host eggs were 24-h old (table 1) ($F = 486.44$; df = 3, 35; $P = 0.0001$). The mean sex ratio showed a definite trend (table 1), suggesting that host age had an effect on the sex ratio of the *T. grandis* offspring ($F = 327.07$; df = 3, 35; $P = 0.0001$).

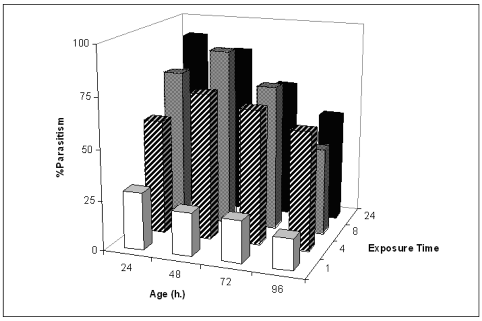

Figure 2. Effect of host age (h) and exposure time (h) on parasitism of Sunn pest egg masses by *T. grandis* at 25 ± 0.5 ºC, 65 ± 5% RH and 16: 8 (L: D) photoperiod.

Table 1. Effect of Sunn pest egg mass age on % parasitism, % parasitoid emergence, and sex ratio of *T. grandis* at 25 ± 0.5 ºC, 65 ± 5% RH and 16: 8 (L: D) photoperiod.

Host age (hour)	% Parasitism	% of emerged parasitoids	Sex ratio (♂/♀ + ♂)
24	91.07 ± 3.54 a	88.48 ± 0.24 a	0.13 ± 0.01 a
48	84.64 ± 7.28 a	81.07 ± 0.40 b	0.19 ± 0.01 b
72	68.21 ± 11.24 ab	59.79 ± 1.26 c	0.46 ± 0.02 c
96	51.79 ± 4.36 b	66.21 ± 0.39 d	0.52 ± 0.01 d

The means within columns followed by different letters are significantly different ($P < 0.01$, Duncan).

Developmental time

Developmental time from oviposition to adult emergence of *T. grandis* in eggs of Sunn pest ranged from 9 to 13 d. The mean developmental times were 11.091 ± 0.1 and 9.68 ± 0.15 d. for female and male, respectively. The average developmental time was shorter for *T. grandis* males compared to that of females.

Adult life parameters

The average life span of males and females ovipositing on the Sunn pest eggs was 40 ± 17.8 and 28.4 ± 15.9 d. (M ± SD), respectively. The average oviposition period was 23.6 ± 11.8 d. Moreover, the females produced 262.2 ± 8.17 eggs throughout their lifespan. A summary of the biological parameters of the adults that developed and oviposited on Sunn pest egg masses in the laboratory is given in table 2.

The life expectancy was 11 d. higher in males compared to that of females. The lifetime net fecundity was 181.83 eggs and the average daily egg production was ~ 7 eggs. Survival for both males and females was > 85 % until day 13 (fig. 4), then it decreased steadily from day 13 to 45, and declined at a lower rate beyond day 50. However, more males survived beyond day 30 when compared to females. The longest lived individuals died at day 73 and 59 for males and females, respectively. Egg production was highest from day 1-10 (> 15 eggs / female / day) and decreased steadily from day 10-45 (fig. 5). Similarly, egg hatch rate was > 75 % until day 25 and then declined to < 50 % from day 25 to 55.

Table 2. Biological parameters of adult *T. grandis* reared on Sunn pest egg masses.

Parameter	**Value**
Adult life expectancy e_0 (days):	
Female	34.6
Male	43.6
Reproduction:	
Gross fecundity (eggs/♀)	228.81
Net fecundity (eggs/♀)	181.83
Egg hatch (h_x) (fraction hatch)	0.875
Gross Fertility (fertile eggs/♀)	200.21
Net fertility (fertile eggs/♀)	159.1
Daily egg production (eggs/female/day)	6.93
Daily production of fertile egg (fertile eggs/female /day)	6.1

Population parameters

Table 3 depicts the population parameters and the stable age distribution of *T. grandis* reared on Sunn pest egg masses. The intrinsic rate of increase and the net reproductive rates were 0.342 and 147.9, respectively, indicating a daily increase of 34.2 % and about a 150-fold increase from generation to generation.

Table 3. Population parameters of *T. grandis* reared on Sunn pest egg masses.

Parameter	**Value**
Rates:	
Net reproductive rate (R_0) (♀/gen)	147.9
Intrinsic rate of increase (r) (1/time)	0.342
Finite rate of increase (λ) (per day)	1.408
Intrinsic rate of birth (b) (1/time)	0.345
Intrinsic rate of death (d) (1/time)	0.003
Times:	
Doubling time (DT) (days)	2.027
Mean generation time (T) (days)	14.61
Age distribution (%):	
Immature stage	0.99
Adult	0.01

The population size was estimated to double in 2 d, while the mean generation time was 14.6 d. Surprisingly, immature constructed 99% of the population developing from Sunn pest egg masses. Therefore, adults represented only 1 % of the population. When 24-h Sunn pest egg masses were provided every 24-h throughout the lifespan of the parasitoids, the highest daily progeny production occurred during the few first days of adult life, followed by a steep decline (fig. 3). After 10 days, a steep decrease in oviposition of females occurred. Production of male progeny, however, remained relatively constant over this time period, representing an increasingly greater proportion of total progeny toward the end of the reproductive cycle.

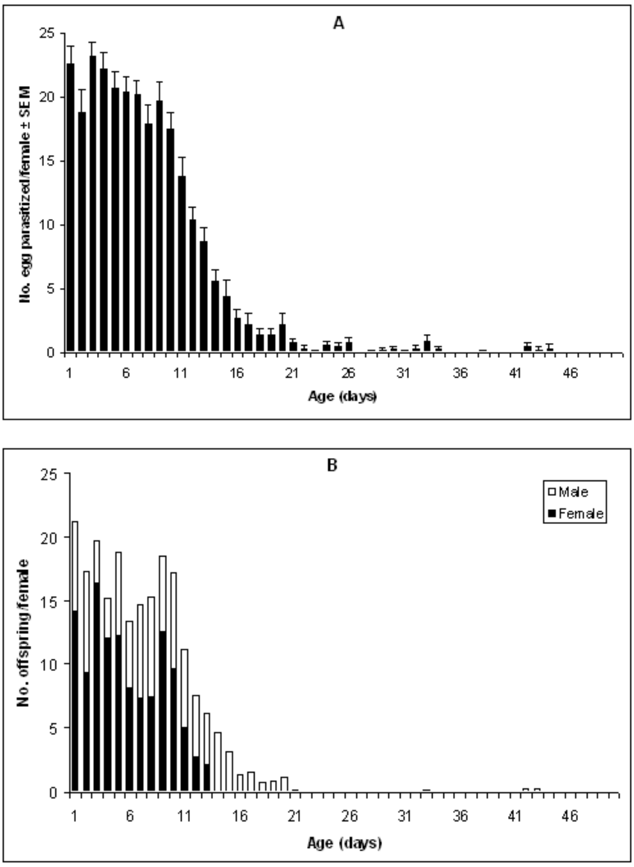

Figure 3. A. The number of Sunn pest egg masses parasitized by female *T. grandis* versus age of females; B. fecundity (m_x) of female parasitoids.

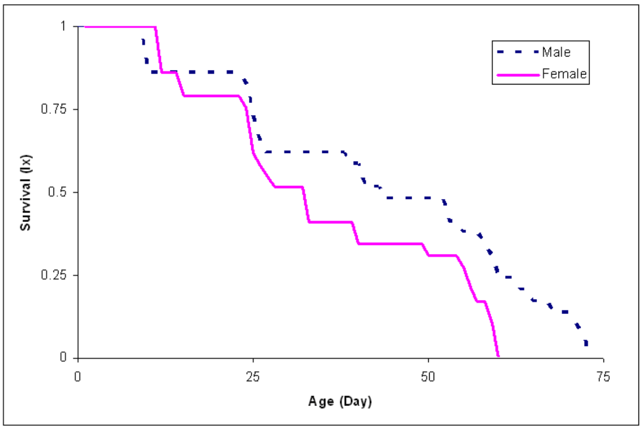

Figure 4. Age specific survival of female and male *T. grandis* reared on Sunn pest egg masses.

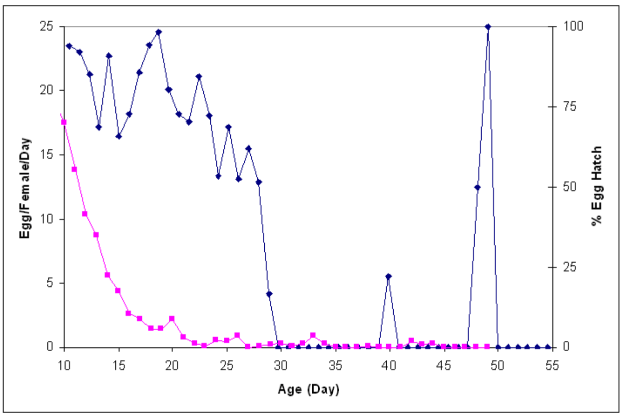

Figure 5. Age specific oviposition and egg hatch rate of *T. grandis* reared on Sunn pest egg masses.

Discussion

Regarding the parasitoid: host ratio and host age effects on the parasitisms and sex ratio of progenies the obtained results are in agreement with those of Jubb & Watson (1971) on *Telenomus utahensis* Ashmead, Hafez *et al*. (1977) on *Platytelenomus hylas* Nixon, Powell &

Shepard (1982) on *Trissolcus basalis* (Wollaston), Dass & Parshad (1983) on *Telenomus remus* Nixon, Ohno (1987) on *Trissolcus plautlae* Watanabe, and Navasero & Oatman (1989) on *Telenomus solitus* Johnson. Wylie (1963), Lingren (1970), Smilowitz & Iwantsch (1975), Nechols & Tauber (1977), Orr *et al.* (1986), Yooichi & Honda (2001), Nakamura & Noda (2002), He & Wang (2006) and Knat *et al.* (2008). These authors noted that host acceptability and suitability may vary with host age. Askew (1971) reported that the effect of host age on the developmental of parasites could be variable. The prominent finding of the present investigation was the achievement of an efficient technique for rearing *T. grandis* in the laboratory by using one d-old Sunn pest egg masses at a ratio of 2 egg masses to 1 female parasitoid, and a 24-h exposure time. The low ratio of hosts to parasitoid was essential to obtain a parasitism rate of > 90%.

Considering the growth and development of immature stages, the observation are similar to those previously reported for *T. grandis* (Safavi, 1968; Amir-Maafi, 2000; Amir-Maafi *et al.*, 2002). It should be noted that *T. grandis* is arrhenotokous, like most scelionids, it is also a solitary parasite, only 1 individual reaching maturity in each host egg (Safavi, 1968; Amir-Maafi, 2000; Amir-Maafi *et al.*, 2002). The female wasp discriminates parasitized from nonparasitized hosts (Safavi, 1968; Amir-Maafi, 2000).

This study also provided demographic data for *T. grandis*. Studies on the biology and demography are important in developing population models and sampling methods in understanding intra and inter-specific relationships and in developing and applying new control methods (Levins & Wilson, 1980). Observing the highest reproduction in early days of adult emergence could be due to ovarian maturity at the time of adult emergence (Voegele, 1961; Wilson, 1961; Safavi, 1968; Amir-Maafi, 2000; Amir-Maafi *et al.*, 2002). However, an apparent, albeit short, pre-ovipositional period has been noted in other scelionids (Javahery, 1967; Powell & Shepard, 1982; Yeargan, 1982; Navasero & Oatman, 1989).

Similar to previous studies (Safavi, 1968; Amir-Maafi, 2000), reporting a female biased a sex ratio for *T. grandis*, more than > 60% of the emerged progenies were females which mated with sibling males soon after emergence. Female bias sex ratios of isolated organisms may help reduce competition among males for mates. Emerging males may commonly mate with their sisters. In the laboratory, male *T. grandis* is routinely seen near egg masses waiting for females of the same cohort to emerge. These reproductive characteristics are common in Scelionidae (Voegele, 1961; Wilson, 1961; Safavi, 1968; Volkoff & Colazza, 1992; Colazza & Bin 1995; Amir-Maafi, 2000). Sibling mating and female bias in sex ratios are cornerstones to theories of local mate competition (Hardy, 1994). These reproductive strategies may have evolved in gregarious or solitary parasitoids that emerge in spatial isolation from potential mates (Hardy, 1994). However, as the female aged, the proportion of male progenies increased. Other scelionids also have been shown to produce a preponderance of female progeny near the beginning of their reproductive period, followed by an increasing proportion of male progeny being produced (Schwartz & Gerling, 1974; Powell & Shepard, 1982). The male biased sex ratio may be the result of a variety of factors, including sperm depletion, sperm death, physiological aging, active sperm digestion by the female, sperm disintegration while stored in the spermathecae, the number of copulations and the differential mortality of the sexes during larval development (Fuester *et al.*, 2003; Gunduz & Gulel, 2005).

Findings on the fertility table were reported for the first time in *T. grandis*. Preliminary observations suggest that the species could be of high importance among natural enemy complex of Sunn pest which promise great potential of *T. grandis* for biological control of the pest. The female biased sex ratio is a positive feature which may improve establishment rates and population growth since *T. grandis* has a relatively high attack rate and long life span. Therefore, small numbers would be needed for augmentative release, especially, when the target pest populations are high. Therefore, this parasitoid may be an excellent practical choice for biological control of Sunn pest. However, testing *T. grandis* in the field is essential in various climate regions to better understanding its value in large-scale release programs.

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References

Amir-Maafi, M. (2000) An investigation on the host-parasitoid system between *Trissolcus gran*dis Thomson (Hym.: Scelionidae) and Sunn pest eggs. Ph. D. Thesis. 220 pp. University of Tehran, Iran.

Amir-Maafi. M., Kharazi-Pakdel, A., Sahragard, A. & Rasolian, G. H. (2002) Study on the biology of *Trissolcus grandis* Thomson (Hym.: Scelionidae) under laboratory condition. *Applied Entomology and Phytopathology* 68, 29-41.

Amir-Maafi, M. & Parker, B. L. (2002) Density dependence of *Trissolcus* spp. (Hym.: Scelionidae) on eggs of *Eurygaster integriceps* Puton [Het.: Scutelleridae]. *Arab Journal of Plant Protection* 20, 62-64.

Amir-Maafi, M. & Parker, B. L. (2003) Efficiency of *Trissolcus* spp. (Hym.: Scelionidae) as an egg parasitoids of *Eurygaster integriceps* Puton [Het.: Scutelleridae] in Iran. *Arab Journal Plant Protection* 21, 69-72.

Anonymous (2007) *Annual report of Sunn pest control in Iran*. 50 pp. Published by Plant Protection Organization. [In Persian].

Askew, R. R. (1971) *Parasitic insects*. 316 pp. American Elsevier, New York.

Carey, J. R. (1993) *Applied demography for biologists*. 224 pp. Oxford University Press, New York.

Colazza, S. & Bin, F. (1995) Efficiency of *Trissolcus basalis* (Hymenoptera: Scelionidae) as an egg parasitoid of *Nezara viridula* (Heteroptera: Pentatomidae) in Central Italy. *Environmental Entomology* 24, 1703-1707.

Critchely, B. R. (1998) Literature review of Sunn pest, *Eurygaster integriceps* Puton. (Hemiptera: Scutelleridae). *Crop Protection* 4, 271-287.

Dass, R. & Parshad, B. (1983) Influence of age of *Spodoptera litur*a (Fabricius) eggs on parasitization by *Telenomus remus* Nixon (Hymenoptera: Scelionidae). *Journal of Entomological Research* 7, 18-20.

Fuester, R. W., Swan, K. S., Dunning, K., Taylor, P. B. & Ramaseshiah, G. (2003) Male-biased sex ratios in *Glyptapantales flavicoxis* (Hymenoptera: Braconidae), a parasitoid of the gypsy moth (Lepidoptera: Lymantriidae). *Annals of the Entomological Society of America* 96, 553-559.

Gunduz, E. A. & Gulel, A. (2005) Investigation of fecundity and sex ratio in the parasitoid *Bracon hebetor* Say (hymenoptera: Braconidae) in relation to parasitoid age. *Turkish Journal of Zoology* 29, 291-294.

Gusev, G. V. & Shmettser, N. V. (1977) Effect of ecological factors on the rearing of telenomines in artificial conditions. *Trudy Vsesoyuznogo Nauchno Issledovatel'skogo Instituta Zashchity Rastenii* 44, 70-82.

Hafez, M., El-Kifl, A. & Fayad, Y. H. (1977) On the bionomics of *Platytelenomus hylas* Nixon, an egg parasite of *Sesamia cretica* Led. in Egypt. *Bulletin de la Société Entomologique d'Égypte* 61, 161-178.

Hardy, I. C. W. (1994) Sex ratio and mating structure in the parasitoid Hymenoptera. *Oikos* 69, 3-20.

He, X. Z. & Wang, Q. (2006) Host age preference in *Aphidius ervi* (Hymenoptera: Aphididae). *New Zealand Plant Protection* 59, 195-201.

Javahery, M. (1967) The biology of some Pentatomoidea and their egg parasites. Ph. D. Thesis. 475 pp. University of London.

Jubb, J. L. & Watson, T. F. (1971) Parasitization capabilities of the pentatomid egg parasite *Telenomus utahensis*. *Annals of the Entomological Society of America* 64, 452-456.

Knat, R., Sandanayaka, W. R. M., He, X. Z. & Wang, Q. (2008) Effect of host age on searching and oviposition behaviour of *Diaeretiella rapae* (M'Intosh) (Hymenoptera: Aphididae). *New Zealand Plant Protection* 61, 355-361.

Levins, R. & Wilson, M. (1980) Ecological theory and pest management. *Annual Review of Entomology* 25, 287-308.

Lingren, P. D. (1970) Hosts and host age preference of *Campoletis perdistinctus*. *Journal of Economic Entomology* 63, 518-522.

Nakamura, A. & Noda, T. (2002) Effects of host age and size on clutch size and sex ratio of *Oomyzus sokolowskii* (Hymenoptera: Eulophidae), a larval-pupal parasitoid of *Plutella xylostella* (Lepidoptera: Yponomeutidae). *Applied Entomology and Zoology* 37, 319-322.

Navasero, R. C. & Oatman, E. R. (1989) Life history, immature morphology and adult behavior of *Telenomus solitus* (Hymenoptera: Scelionidae). *Entomophaga* 34, 165-177.

Nechols, J. R. & Tauber, M. J. (1977) Age-specific interaction between the greenhouse whitefly and *Encarsia formosa* influence of host on the parasite's oviposition and development. *Environmental Entomology* 6, 143-149.

Ohno, K. (1987) Effect of host age on parasitism by *Trissolcus plautlae* Watanabe (Hymenoptera: Scelionidae) an egg parasitoid of *Plautla stali* Scott. (Heteroptera: Pentatomidae). *Applied Entomology and Zoology* 22, 646-648.

Orr, D. B., Russin, J. S. & Borthel, D. J. (1986) Reproductive biology and behavior of *Telenomus calvus* (Hymenoptera: Scelionidae), a phoretic egg parasitoid of *Podisus maculiventris* (Hemiptera: Pentatomidae). *Canadian Entomologist* 118, 1063-1072.

Powell, J. E. & Shepard, M. (1982) Biology of Australian and United State strains of *Trissolcus basalis*, a parasitoid of the green vegetable bug, *Nezara viridula*. *Australian Journal of Ecology* 7, 181-186.

Safavi, M. (1968) Etude biologique et écologique des Hyménoptères parasites des oeufs des punaises des céréales. *Entomophaga* 13, 381-495.

SAS Institute (1987) *SAS user's guide*: *statistics*. SAS Institute, Carey, N.C.

Schwartz, A. & Gerling, D. (1974) Adult biology of *Telenomus remus* under laboratory conditions. *Entomophaga* 19, 483-492.

Shahrokhi, Sh. (1997) A study on mass rearing of *Trissolcus grandis* on *Graphosoma lineatum* eggs and quality control for biological control of Sunn pest, *Eurygaster integriceps* Put. (Hem.: Scutelleridae). M. Sc. Thesis. 110 pp. University of Tehran, Iran.

Shapiro, V., Gusev, G. V. & Kapustina, O. V. (1975) Comparative evaluation of the biological properties of egg parasites of the family Scelionidae, both introduced and indigenous species. *Trudy Vsesoyuznogo Nauchno Issledovatel'skogo Instituta Zashchity Rastenii* 44, 57-69.

Shirazi, J. (2006) Investigation on the *in vitro* rearing of *Trisslcus grandis* an egg parasitoid of *Eurygaster integriceps* by use of artificial diet. *Pakistan Journal of Biological Science* 9, 2040-2047.

Smilowitz, Z. & Iwantsch, G. F. (1975) Relationships between the parasitoid *Hyposoter exiguae* and cabage looper, *Trichoplusia ni*: the effect of host age on ovipositional rate of the parasitoid and successful parasitism. *Canadian Entomologist* 107, 689-694.

Taghadosi, M. (1991) A comparison study on reproductive potentials of Karaj, Ghazvin, Varamin and Shahriar populations of *Trissolcus grandis* Thom. (Hym.: Scelionidae) on eggs of Sunn pest, *Eurygaster integriceps* Put. (Hem.: Scutelleridae) M. Sc. Thesis. 138 pp. University of Tehran, Iran.

Voegele, J. (1961) Contribution a' l'etude de la biologie des Hymenopteres oophages des punaises des cereals au Maroc. *Cahiers de la Recherche Agronomique* [*Rabat*] 14, 69-90.

Volkoff, N. & Colazza, S. (1992) Growth patterns of teratocytes in the immature stages of *Trissolcus basalis* (Woll.) (Hymenoptera: Scelionidae), an egg parasitoid of *Nezara viridula* (L.) (Heteroptera: Pentatomidae). *International Journal Insect Morphology* 21, 323-336.

Wilson, F. (1961) Adult reproductive behaviour in *Asolcus basalis* (Hym.: Scelionidae). *Australian Journal Zoology* 9, 737-751.

Wylie, H. G. (1963) Some effects of host age on parasitism of *Nasonia vitripennis* (Walk.) [Hymenoptera: Pteromalidae]. *Canadian Entomologist* 95, 881-856.

Yeargan, K. V. (1982) Reproductive capability and longevity of the parasitic wasps *Telenomus podisi* and *Trissolcus euschisti*. *Annals of the Entomological Society of America* 75, 181-183.

Yooichi, K. H. & Honda, H. (2001) Effect of host pupal age on host preference and host suitability in *Brachymeria lasus* (Walker) (Hymenoptera: Chalcididae). *Applied Entomology and Zoology* 36, 97-102.

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