

Effect of Host Availability and Egg Load in *Trichogramma platneri* Nagarkatti (Hymenoptera: Trichogrammatidae) and Its Consequences on Progeny Quality

Celso L. Hohmann^{1,2*} and Robert F. Luck¹

¹ University of California; CA 92521; Riverside - USA. ² Instituto Agrônômico do Paraná - IAPAR; cel Luiz@iapar.br; C. P. 481; 86001-970; Londrina - PR - Brazil

ABSTRACT

Experiments were conducted to determine whether *Trichogramma platneri* Nagarkatti manifested a somatic-gametic trade-off and whether it was affected by host availability and host size. Large wasps produced on *Trichoplusia ni* Hübner and limited to five or 15 *T. ni* eggs daily, produced a similar number of progeny as wasps offered hosts from emergence. Similar results were obtained when they were deprived of *T. ni* eggs for one, three, five, or ten days and then provided with unlimited hosts daily until death. In contrast, small wasps produced from *Sitotroga cerealella* (Olivier) and deprived of *T. ni* eggs for one to three days suffered a significant reduction in progeny production. Regardless of size, the egg load of non-ovipositing wasps increased significantly with time and a positive relationship existed between the life span of a female and the length of time she was deprived of hosts.

Key words: Biological control, somatic-gametic trade-off, reproductive success

INTRODUCTION

When parasitoids are released, their ability to find hosts and to manipulate their egg load and life span in response to host availability will determine their efficacy as an augmentative biological control agent. Natural enemies may not be able to find hosts immediately after release, or the hosts may be scarce or unsuitable. Under these conditions, the physiological state of the female (i.e., an appropriate balance of resources to be allocated to reproduction versus survival) has important implications for its reproductive success.

It is known that ovipositing females adjust their clutch size and gender according to the rate and quality of the hosts they encounter during their

lifetime (Salt, 1934; Waage and Ng, 1984; Godfray, 1994; Heimpel and Collier, 1996).

However, the decision of whether or not to parasitize a host depends on the number of mature eggs in the female's ovaries and her age (Donaldson and Walter, 1988; Trudeau and Gordon, 1989; Minkenberg et al., 1992; Godfray, 1994).

Species of *Trichogramma* (Hymenoptera: Trichogrammatidae) have been considered proovigenic (Pak and Oatman, 1982) and if hosts are abundant, nearly all of their eggs are laid in the first few days of life (Pak et al., 1985, Hohmann et al., 1988; Fleury and Bouletreau, 1993). Pak et al. (1985), however, speculated that under host scarcity conditions, females might be able to continue searching over an extended period of

* Author for correspondence

time by controlling the ovulation and ovisorption processes. Bai and Smith (1993) showed that *Trichogramma minutum* Riley females when provided limited *Ephestia kuehniella* (Zeller) (Lepidoptera: Pyralidae) eggs per day laid their eggs more evenly throughout their lifetime than females provided an unlimited number of hosts per day. Females provided with unlimited hosts laid most of their eggs in the first three days of life. Furthermore, Pak et al. (1985) reported that *Trichogramma* spp., with a full complement of mature eggs, walked faster when foraging for hosts, and searched longer than females with fewer eggs. Thus, the ability of *Trichogramma* females to find hosts and manage their fecundity in response to changing host resources is key to their effectiveness as biological control agents in the field.

Studies with different taxa have shown that organisms that invest more in reproduction effort may reduce their life expectancy as a result of a somatic-gametic trade-off (Reznick, 1985; Bell and Koufopanou, 1986; Stearns, 1992). Although the reduction in parental life span with increasing reproductive investment is generally accepted, little evidence of such a trade-off exists for parasitic Hymenoptera. The only evidence in *Trichogramma* suggests that a positive correlation exist between reproduction and life span, i. e., wasps provided hosts lived longer than those without hosts (Lund, 1938; Bai and Smith, 1993).

To understand how host size, through its effect on offspring size, affects a parasitoid's reproductive prospects, under different conditions of host availability, experiments were carried out to determine: a) whether host availability and female's egg load affects progeny production and survival of *T. platneri* and b) whether host size affects wasp's somatic-gametic trade-off between longevity and fecundity.

MATERIAL AND METHODS

Host Cultures

Eggs of the cabbage looper, *Trichoplusia ni* Hübner (Lepidoptera: Noctuidae) and the Angoumois grain moth, *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae) were used as hosts for *T. platneri*. Cabbage looper eggs were obtained daily from a colony maintained at the University of California, Riverside, on artificial diet developed by Shorey and Hale (1965) as

modified by Pak and Oatman (1982). *S. cerealella* eggs were provided by Rincon-Vitova Insectaries, Ventura, California. The cabbage looper and the Angoumois grain moth eggs were placed in a cobalt 60 source irradiator for 40 min to prevent cannibalism. After irradiation the eggs were stored up to 24h in a refrigerator at $6\pm 1^{\circ}\text{C}$ before being used in the experiments.

Parasitoid Culture

Trichogramma platneri was obtained from an *Amorbia cuneana* Wals. (Lepidoptera: Tortricidae) egg-mass collected on an avocado tree, *Persea americana* Miller, near Porterville, California, July, 1993. The wasps from this egg-mass (91 individuals) were used to initiate a culture by placing a parasitized egg-mass within a standard parasitoid rearing unit (9.5 x 2.5-cm glass shell vial). The open end of the vial was sealed with a filter paper disk held in place by polyethylene lid with a hole, 1.8 cm in diam., cut in its center. When the parasitoids emerged, strips of toweling containing several hundred *T. ni* eggs were exposed to the parasitoids inside the glass shell vial. Seven cultures were started, each on different days, to provide wasps to initiate experiments.

Female size

In all experiments, female size was determined by mounting the wasps on a glass microscope slide in Hoyer's medium and the length of one of the hind tibiae (HTL) measured. The HTL was used as an index of wasp size (Waage and Ng, 1984; Hohmann et al., 1988).

Female Egg Load

To determine the female's egg load, the wasp was killed by freezing and her abdomen separated from her body in a small drop of Ringer's insect saline, on a microscope slide, using fine dissecting needles. The ovaries were then dissected out and the eggs were gently separated. As the saline dried, a drop of acid fuschin (Maple, 1947) was added to stain the eggs. After the staining was completed (ca. 1 min.) the eggs were mounted in Hoyer's medium and their number counted for each female at 200X under a compound microscope.

Experimental Protocol

Host Scarcity Effect on Wasp Fecundity and Longevity

Newly emerged *T. platneri* females, reared on *T. ni* eggs were randomly selected at emergence and assigned to one of the three host densities cards: unlimited, 15, and five hosts, inside experimental units (9.5 x 2.5-cm glass shell vial). The egg cards were replaced daily until female's death. Eleven replicates were used. The number of offspring produced by each female each day and the female's life span were determined.

Host Deprivation Effects on Wasp Fecundity and Longevity

Newly emerged large (reared on *T. ni* eggs) and small (reared on *S. cerealella* eggs) *T. platneri* females were randomly selected at emergence. Each female was isolated in a gelatin capsule (#000 size) streaked with honey and assigned to one of five treatment groups based on the number of days that she was to be deprived of hosts. Wasps reared from *T. ni* were deprived of hosts for 0 (n = 11), 1 (n = 12), 3 (n = 10), 5 (n = 9), and 10 (n = 10) days. Those reared from *S. cerealella* were deprived of hosts for 0 (n = 13), 1 (n = 16), 3 (n = 10), and 5 (n = 11) days. Wasps reared from *S. cerealella* died before attaining ten days of host deprivation. On the appropriate day, each female was transferred to a vial (9.5 x 2.5 cm) containing more than 50 *T. ni* eggs. The cards, containing the host eggs were replaced daily until female's death. The parental females' lifetime progeny produced, their brood size, and their gender were recorded. The life span of each parental female was also determined.

Temporal Egg Load

To determine the temporal change in a female's egg load during her lifetime, female wasps emerging from *T. ni* or *S. cerealella* eggs were randomly selected at emergence and isolated in a gelatin capsule streaked with honey. Each *T. ni* derived wasp was assigned to one of the seven treatments (n = 30): zero, one, three, five, seven, ten, or 15 days. Each *S. cerealella* derived wasp was assigned to one of the six treatments: 0 (n = 26), 1 (n = 25), 3 (n = 26), 5 (n = 25), or 7 (n = 25) days. Most of the wasps reared from *S. cerealella* lived less than ten days. The treatments were based on the number of days since the female's emergence. On the appropriate day, the wasps

from each group were frozen, their ovarian eggs were counted and a hind tibia length was measured.

The colonies as well as the experiment units were maintained at 28±1°C, 50±10% RH, 16D:8L. Honey was streaked on the inside of the vials as a carbohydrate source.

Statistical Analysis

Treatment effects on life span and lifetime progeny production were evaluated using analysis of covariance (ANCOVA) (GLM procedure, SAS Institute Inc., 1994). The same analysis was used when the egg load was determined. The fecundity data were square root transformed, $\sqrt{x + 0.5}$, and the hind tibia length was transformed using natural logarithms, $\ln(x)$. Egg load, sex ratio and brood size data were analyzed using a one-way analysis of variance (ANOVA) (GLM procedure, SAS Institute Inc. 1994). Sex ratio data were arcsine transformed before analysis (Zar, 1984).

RESULTS

Host Scarcity Effect on Fecundity and Longevity of *T. platneri* Reared on *T. ni* Eggs

The lifetime fecundity and life span of wasps were unaffected by the number of hosts they were offered per day, i.e., five, 15, or unlimited hosts ($F_{[2, 23]} = 0.08$, $P > 0.05$). The number of progeny produced by females offered unlimited, 15 or five hosts per day was 74.6, 83.2, and 61.7, respectively (Table 1). The cumulative offspring produced during the first three days by *T. platneri* in the three treatments (Fig. 1) differed significantly ($F_{[2, 30]} = 6.81$, $P < 0.005$); wasps offered five or 15 hosts per day produced fewer offspring (29.4±8.2 and 14.9±4.0, respectively) than did those offered unlimited hosts (53.2±7.2). However, those wasps offered limited hosts laid more progeny during subsequent days (5 hosts: 46.4±6.2; 15 hosts: 53.8±10.5) than did those with unlimited hosts (20.3±3.7). Consequently, lifetime fecundity of similarly sized wasps did not differ significantly regardless whether they were offered five, 15, or unlimited hosts per day ($F_{[2, 26]} = 2.65$, $P > 0.05$). The number of parasitoids produced per host was inversely related to the number of available hosts.

Significantly more parasitoids emerged per host when the females only had access to five and 15

eggs per day than when they had unlimited host eggs ($F_{[2,30]} = 15.94$, $P < 0.001$) (Table 1). Also, parental females that had access to unlimited hosts per day produced significantly more daughters than did females of similar size when they were provided with either five or 15 hosts daily ($F_{[2,30]} = 7.67$, $P < 0.005$) (Table 1).

The age-specific survival of *T. platneri* provided different *T. ni* egg densities are shown in Figure 2. Wasps supplied five or 15 hosts per day lived 17.8 and 15.3 days, respectively, whereas those

supplied unlimited hosts lived 11.3 days (Table 1). The differences, however, were not significant ($F_{[2,29]} = 2.51$, $P > 0.05$) when wasp size was included in the analysis. When the longevity of females provided unlimited hosts was compared with that of females provided five hosts per day, a significant difference was found ($F_{[1,17]} = 10.9$, $P < 0.005$). This difference, however, was likely explained by the interaction between wasp size and progeny (See Table 2).

Table 1 - Effect of host availability on life history attributes ($\bar{x} \pm s.e.$) of *T. platneri* on *T. ni* eggs.

No. eggs/female	n	HTL parental female (mm)	Lifetime progeny	% of females	Brood size	Longevity (days)
Unlimited	11	0.166 \pm 0.006a ¹	74.6 \pm 10.2a	76a	1.4 \pm 0.2c	11.3 \pm 2.8a
15	11	0.204 \pm 0.005c	83.2 \pm 7.4a	65c	1.8 \pm 0.2b	15.3 \pm 4.8a
5	11	0.183 \pm 0.008b	61.7 \pm 7.2a	72b	2.0 \pm 0.3a	17.8 \pm 5.0a

¹Means followed by the same letter in the columns are not significantly different (Duncan's Multiple Range Test; see levels in the text).

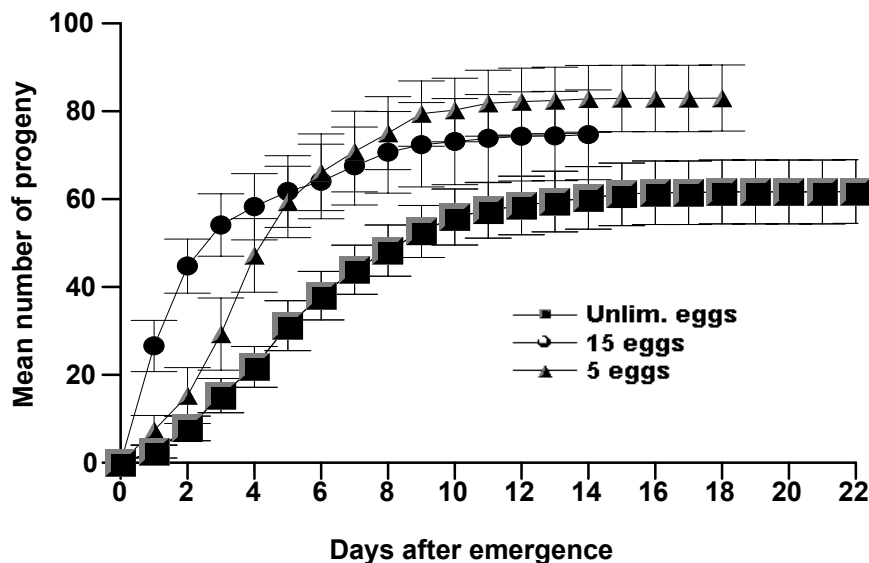


Figure 1 - Cumulative progeny produced by *T. platneri* exposed to different *T. ni* egg densities.

Effect of Host Deprivation on Fecundity and Longevity of *T. platneri* Reared on *T. ni* Eggs

Females offered hosts for their entire lives produced 50% less offspring during the first day of oviposition than did those deprived of hosts for one, three, five or ten days. However, they did not differ from their deprived counterparts in the total number of progeny they produced ($F_{[4,47]} =$

0.56, $P > 0.05$) (Table 3). Thus, host deprivation of up to ten days did not affect the lifetime fecundity of similarly sized wasps. Temporary host deprivation also did not affect the number of offspring emerging per host ($F_{[4,47]} = 1.60$, $P > 0.05$) (Table 3).

No clear relationship existed between the period of host deprivation and the percentage of female

offspring (Table 3). Although wasps maintained without hosts for ten days produced the fewest females, the difference was not significant ($F_{[4,46]}=1.28$, $P>0.05$).

A direct relationship existed between a female's life span and host deprivation period (Table 3). Wasps with unlimited hosts lived significantly less than those deprived of hosts for one, five, and ten days ($F_{[4,41]} = 3.30$, $P<0.01$) (Table 3). Among females withheld from hosts, those maintained in the absence of eggs for ten days before they were allowed to oviposit lived the longest.

Temporal Egg Load of *T. platneri* Reared on *T. ni* Eggs

In the absence of hosts, the egg load of *T. platneri* changed significantly with time ($F_{[6, 299]} = 17.02$, $P<0.001$) (Fig. 3). Egg load increased until the fifth day after emergence and then declined. Wasps at emergence had approximately 65% of the egg load of a 1-day old female, 50% of the egg load of 3 and 5-day old females, and 55% of the egg load of 7 and 10-day old females. After 15 days, the number of eggs present in the female's ovaries was similar to that found in newly emerged wasps.

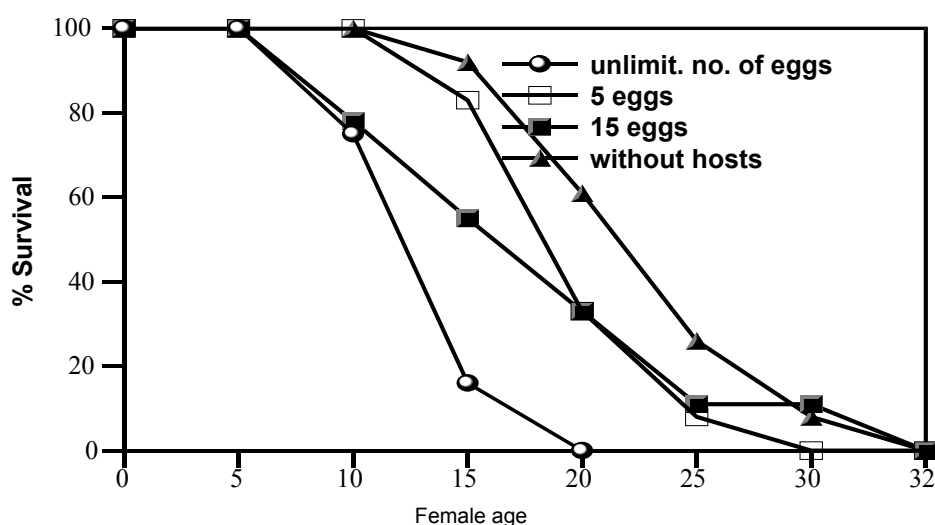


Figure 2 - Age-specific survival of *T. platneri* provided with different *T. ni* egg densities.

Table 2 - Effect of host density (HD) on the longevity of *T. platneri* exposed to *T. ni* eggs¹.

Character	DF	SS	MS	F-value	P>F
HD	1	0.6525	0.6525	10.96	0.004
PROG	1	0.3862	0.3862	6.49	0.020
HTL	1	0.3173	0.3173	5.33	0.033
PROG*HL	1	0.3886	0.3886	6.53	0.020

¹Results were analyzed by an ANCOVA using hind tibia length (HTL) and progeny (PROG) as covariates.

Table 3 - Effect of temporary host deprivation on life history attributes ($\bar{x} \pm \text{s.e.}$) of *T. platneri* on *T. ni* eggs.

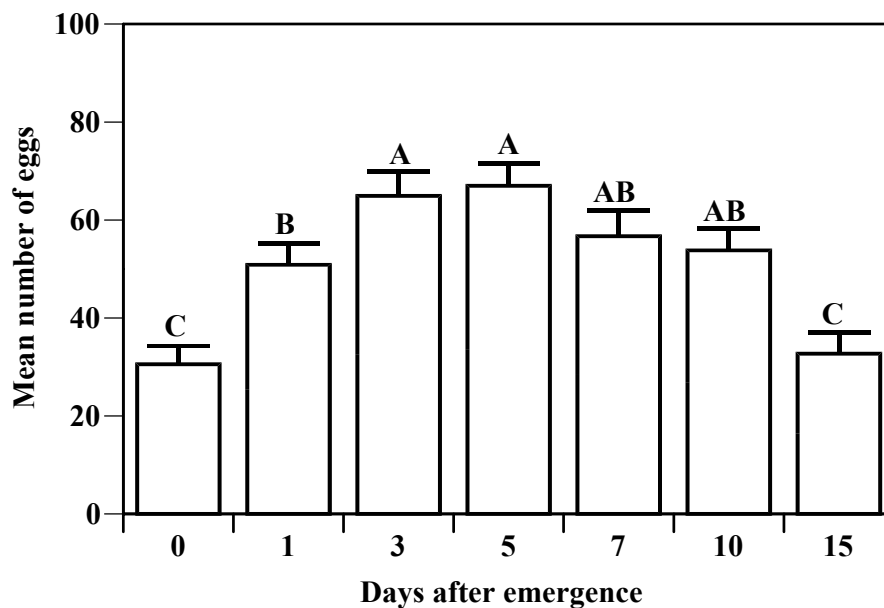
Days without hosts	n	HTL parental female (mm)	Lifetime progeny	% of females	Brood size	Longevity (days)
0	11	0.166±0.006a ¹	74.6±10.2a	76a	1.4±0.2a	11.3±2.8a
1	12	0.172±0.005a	74.7± 9.9a	78a	1.3±0.1a	13.9±0.8b
3	10	0.168±0.007a	66.6± 9.2a	81a	1.3±0.2a	12.9±0.7ab
5	9	0.170±0.008a	59.3± 9.1a	76a	1.4±0.2a	15.1±1.7b
10	10	0.178±0.007a	61.6± 8.3a	73a	1.2±0.1a	18.6±0.5c

¹Means followed by the same letter in the columns are not significantly different (Duncan's Multiple Range Test; see levels on the text).

Table 4 - Effect of temporary host deprivation on life history attributes ($\bar{x} \pm \text{s.e.}$) of *T. platneri* reared on *S. cerealella* eggs for one generation.

Days without hosts	n	HTL parental female (mm)	Lifetime progeny	% of females	Brood size	Longevity (days)
0	13	0.158±0.002a1	62.2±4.04a	63a	1.4±0.03ab	9.0±2.2a
1	16	0.151±0.002a	44.6±5.02a	53a	1.2±0.03b	10.5±0.7a
3	10	0.142±0.003a	26.6±5.2b	52a	1.5±0.18a	10.3±1.1a
5	11	0.158±0.002a	29.2±4.01c	43a	1.3±0.05b	11.4±0.6a

¹Means followed by the same letter in the columns are not significantly different (Duncan's Multiple Range Test; see levels on text).

**Figure 3** - Temporal egg load of *T. platneri* reared on *T. ni* eggs.

Effect of Host Deprivation on Fecundity and Longevity of *T. platneri* Reared on *S. cerealella* Eggs

In contrast to wasps reared on *T. ni* eggs, those reared on *S. cerealella* eggs showed a decrease in progeny production with increasing periods of host deprivation ($F_{[3, 45]} = 8.99$, $P < 0.0001$) (Table 4). Females of similar size deprived of hosts for one, three and five days laid approximately 60% fewer progeny than did females offered hosts since emergence.

Temporary host deprivation affected the number of offspring emerging per host ($F_{[3, 46]} = 3.10$, $P < 0.05$), but did not affect the proportion of female offspring ($F_{[3, 46]} = 3.46$, $P > 0.05$), or a female's life span ($F_{[3, 46]} = 2.72$, $P > 0.05$) (Table 4).

Temporal Egg Load of *T. platneri* Reared on *S. cerealella* Eggs

The number of eggs present in the ovaries of a female deprived of hosts increased during the first day compared to that present in a newly emerged female (Fig. 4). It then remained constant until the seventh day after emergence. The egg load of a 3-day old female represented a 30% increase over that present at emergence, but the difference was not significant ($F_{[4, 112]} = 3.05$, $0.05 > P > 0.01$).

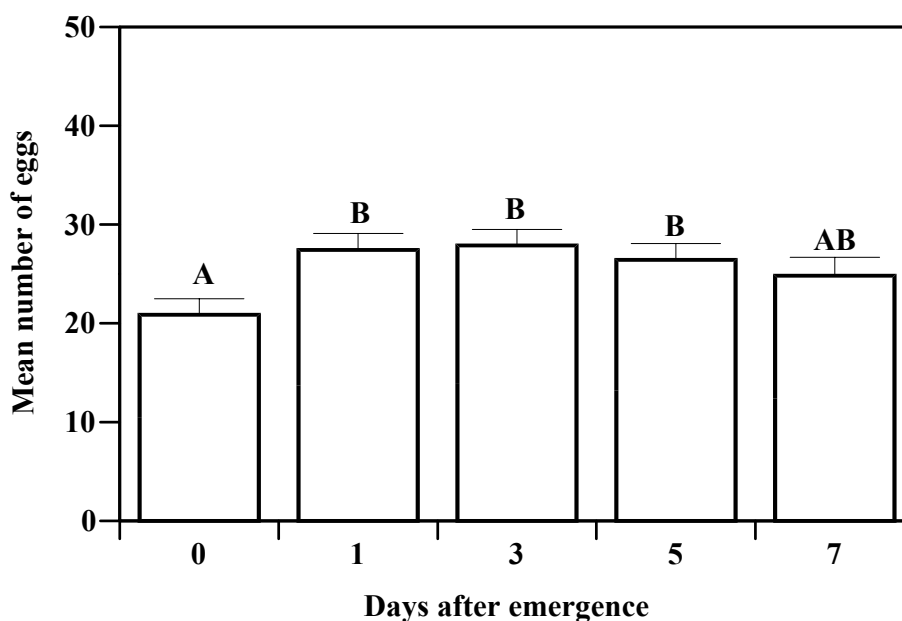


Figure 4 - Temporal egg load of *T. platneri* reared on *S. cerealella* eggs.

DISCUSSION

Trichogramma platneri females responded to variable host availability by changing the pattern of egg laying, from a high reproductive investment early in life to one that was more even distributed throughout the life span without compromising fecundity. High reproductive effort early in life, however, resulted in a decrease in longevity, indicating the existence of a gametic-somatic trade-off. Wasps maintained in the absence of hosts or provided five hosts throughout their lifetimes lived longer than those offered unlimited hosts each day. Pak et al. (1985) hypothesized that when hosts are scarce, *Trichogramma* should manipulate ovisorption and ovulation and thus, regulate the amount of resources allocated to maintenance, i.e., the time available for host search at the expense of fecundity. However, Bai and Smith (1993) found that *T. minutum* females provided unlimited hosts lived longer than either those provided limited hosts or those maintained in the absence of hosts. Lund (1938) also found a positive relationship between host availability and longevity in *Trichogramma evanescens* Westw. These studies, however, failed to consider the effect of host size on longevity.

The response of *T. platneri* females on our study depended fundamentally on whether they were reared on a large (*T. ni*), or a small host (*S. cerealella*). Lifetime progeny production by large females deprived of hosts for one to ten days after emergence differed only slightly (< 20%) from that of females offered hosts since emergence. Temporal changes in both the egg load of *T. platneri* in this study, and of *T. minutum* reared on *T. ni* eggs (CLH, pers. obs.) revealed that females continued to mature eggs until the fifth day after emergence. A two-fold increase occurred in the egg load in both species during this 5-day period. In contrast, depriving small females of hosts for one day after emergence significantly reduced (28%) their progeny production. If small females were withheld from hosts for three days, their number of progeny was reduced by 57%. The more drastic reduction in progeny production by *T. platneri* reared on *S. cerealella* eggs probably resulted from a lower capacity by these females to produce and store eggs for long periods. In these small wasps, the egg load increased only during the first day after emergence and it remained constant thereafter. Fleury and Bouletreau (1993) reported a drastic effect of temporary host deprivation on the parasitization rates of *Trichogramma brassicae* Bezdenko parasitizing *E. kuehniella* eggs when females were deprived of

hosts for more than three days. These workers attributed this effect to the wasp's low ability to store eggs for more than three days. This does not appear to be the reason for the lower progeny production by small *T. platneri* when they were deprived of hosts for various periods. These females maintained a constant number of eggs in their ovaries until the fifth day after emergence. Anunciada and Voegelé (1982), and Volkoff and Daumal (1994) reported a similar result for *T. brassicae*. These workers showed that *T. brassicae* continued to mature eggs until the fourth and fifth day after emergence.

Studies with *T. platneri*, *T. minutum* (CLH pers. obs.), and *T. brassicae* (Anunciada and Voegelé, 1982; Fleury and Bouletreau, 1993; Volkoff and Daumal, 1994) suggest that the classification of *Trichogramma* as a proovigenic species (sensu Flanders, 1950) does not reflect the temporal pattern of either oviposition or egg load changes in these parasitoids. Jervis and Copland (1996) suggested that it would be better to consider proovigeny and synovigeny as extremes in a continuum since, among insects, there are varying degrees of synovigeny.

The effects of initial host deprivation on longevity depended on the size of the wasp. A direct relationship existed between host deprivation and longevity for large wasps (reared on *T. ni* eggs). The longer those larger females were deprived of hosts, the longer they lived. In contrast, no relationship was found for small wasps (reared on *S. cerealella* eggs). The increased longevity of large *T. platneri* when temporarily deprived (this study) or when denied hosts for its entire life (Hohmann et al., 1989; McDougall and Mills, 1997; CLH, pers. obs.) in contrast to small wasps, suggests that an interaction exists between life span, egg production and wasp size. It also suggests that small wasps do not allocate as many resources to longevity as large wasps. The amount of resources in large wasps allowed them to survive for long periods without compromising fecundity. This may explain the differences in progeny production between large and small females when deprived of hosts.

Larger females have potentially greater reproductive success than smaller females, confirming the positive correlations between wasp size and some components of fitness investigated in laboratory experiments (Flanders, 1935; Salt, 1940; Klomp and Teerink, 1967; Marston and Ertle, 1973; Waage and Ng, 1984; Hohmann et al.,

1988). However, Kazmer and Luck (1995) demonstrated that average postdispersal fitness of adult *T. pretiosum* Riley in the field only increased until *T. pretiosum* reached an intermediate size after which it remained constant. These authors concluded that a linear relationship does not exist between fitness and wasp size. They showed that small wasps are at a substantial disadvantage reproductively. However, they only measured the size of wasps that encountered a host on egg cards, not how long they lived or how many hosts they encountered during their lifetime. Ellers et al. (1998) studied the size-fitness relationships in the parasitoid *Asobara tabida* (Nees) (Hymenoptera: Braconidae). They showed that a correlation existed between a wasp's lifetime reproductive success and its size in the field. Although the size of the wasp may seriously constrain its efficiency as a biological control agent in the field, its effect can be counterbalanced under certain conditions by increasing the number of parasitoids released or by maintaining production of the largest host practicable.

Various studies have been conducted to improve the success of released *Trichogramma*. They have revealed the importance of feeding the wasps a carbohydrate (Yu et al., 1984; Smith et al., 1986; Hohmann et al., 1988, 1989; McDougall and Mills, 1997), exposing them to their target hosts before releasing them (Bergeijk et al., 1989), and timing their release (Volkoff and Daumal, 1994; Smith, 1996). The adoption of these recommendations along with maximizing wasp size would certainly improve current biological control programs that use *Trichogramma* spp.

RESUMO

Experimentos foram conduzidos para determinar se fêmeas de *Trichogramma platneri* Nagarkatti (Hymenoptera: Trichogrammatidae) têm a habilidade de direcionar a alocação de recursos (reprodução/longevidade) e se esse comportamento é afetado pela disponibilidade e pelo tamanho dos hospedeiros. Fêmeas de parasitóides grandes, oriundas de ovos de *Trichoplusia ni* Hübner (Lepidoptera: Noctuidae), expostas a cinco ou 15 ovos de *T. ni*, diariamente, produziram número similar de descendentes que aquelas fêmeas que tiveram acesso a número ilimitado de hospedeiros desde a emergência. Resultados similares foram obtidos quando elas

foram mantidas temporariamente sem ovos de *T. ni* durante um, três, cinco ou dez dias, e então providas com um suplemento ilimitado de hospedeiros. Contrariamente, fêmeas pequenas, oriundas de ovos de *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae), mantidas temporariamente sem ovos de *T. ni* durante um período de um a três dias, apresentaram uma redução significativa no número de descendentes produzidos. Independentemente do tamanho da fêmea, o número de ovos presentes no ovário aumentou significativamente com o transcorrer do tempo. Além disso, existiu uma relação positiva entre longevidade e a duração do período em que as fêmeas foram mantidas na ausência do hospedeiro.

REFERENCES

- Anunciada, L. and Voegelé, J. (1982), L'importance de la nourriture dans le potentiel biotique de *Trichogramma maidis* Pintureau et Voegelé et *Trichogramma nagarkattii* Voegelé et Pintureau (Hym.: Trichogrammatidae) et l'osorption dans les femelles en contention ovarienne. In: *Primier Symposium International*. Les Trichogrammes, Antibes (France), 20-23 avril 1982. Colloq. INRA, **9**, 79-84.
- Bai, B. and Smith, S. M. (1993), Effect of host availability on reproduction and survival of the parasitoid wasp *Trichogramma minutum*. *Ecol. Entomol.*, **18**, 297-286.
- Bell, G. and Koufopanou, V. (1986), The cost of reproduction. *Oxford Surv. Evol. Biol.*, **3**, 83-131.
- van Bergeijk, K. E.; Bigler, F.; Kaashoek, N. K. and Pak, G. A. (1989), Changes in host acceptance and host suitability as an effect of rearing *Trichogramma maidis* on a factitious host. *Entomol. Exp. Appl.*, **52**, 229-238.
- Donaldson, J. S. and Walter, G. H. (1988), Effects of egg availability and egg maturation on ovipositional activity of the parasitic wasps, *Coccophagous atratus*. *Physiol. Entomol.*, **13**, 407-417.
- Ellers, J.; van Alphen, J. J. M. and Sevenster, J. G. (1998), A field study of size-fitness relationships in the parasitoid *Asobara tabida*. *J. Anim. Ecol.*, **67**, 318-324.
- Flanders, S. E. (1935), Host influence and prolificacy and size of *Trichogramma*. *Pan-Pacific Entomol.*, **11**, 175-177.
- Flanders, S. E. (1950), Regulation of ovulation and egg disposal in the parasitic Hymenoptera. *Can. Entomol.*, **82**, 134-140.
- Fleury, F. and Bouletreau, M. (1993), Effects of temporary host deprivation on the reproductive potential of *Trichogramma brassicae*. *Entomol. Exp. Appl.*, **68**, 203-210.
- Godfray, H. C. J. (1994), Parasitoids. Princeton, N. J. : Princeton University Press. 473 pp.
- Heimpel, G. E. and Collier, T. (1996), The evolution of host-feeding behaviour in insect parasitoids. *Biol. Rev.*, **71**, 373-400.
- Hohmann, C. L.; Luck, R. F. and Oatman, E. R. (1988), A comparison of longevity and fecundity of adult *Trichogramma platneri* Nagarkatti (Hymenoptera: Trichogrammatidae) reared from eggs of the cabbage looper and the Angoumois grain moth, with and without access to honey. *J. Econ. Entomol.*, **85**, 1307-1312.
- Hohmann, C. L.; Luck, R. F.; Oatman, E. R. and Platner, G. R. (1989), Effects of different biological factors on longevity and fecundity of *Trichogramma platneri* Nagarkatti (Hymenoptera: Trichogrammatidae). *Ann. Ent. Soc. Brasil*, **18**, 61-70.
- Jervis, M. and Kidd, N. (1996), Insect natural enemies: practical approaches to their study and evaluation. London : Chapman and Hall. 491 pp.
- Kazmer, D. and Luck, R. F. (1995), Size-fitness relationships in field populations of the egg parasitoid, *Trichogramma pretiosum*. *Ecology*, **78**, 412-425.
- Klomp, H. and Teerink, B. J. (1967), The significance of oviposition rates in the egg parasite *Trichogramma embryophagum* Htg. *Arch. Neerl. Zool.*, **17**, 350-375.
- Lund, H. O. (1938), Studies on longevity and productivity of *Trichogramma evanescens*. *J. Agric. Res.*, **56**, 421-439.
- Maple, J. D. (1947), The eggs and the first larvae of Encyrtidae and the morphological adaptations for respiration. *Univ. Calif. Publications in Entomology*, **8**, 25-122.
- Marston, N. and Ertle, L. R. (1973), Host influence on the bionomics of *Trichogramma minutum*. *Ann. Entomol. Soc. Am.*, **66**, 1155-1162.
- McDougall, S. J. and Mill, N. J. (1997), The influence of hosts, temperature and food sources on the longevity of *Trichogramma platneri*. *Entomol. Exp. Appl.*, **83**, 195-203.
- Minkenberg, O. P. J. M.; Tatar, M. and Resenheim, J. A. (1992), Egg load as a major source of variability in insect foraging and oviposition behavior. *Oikos*, **65**, 134-142.
- Pak, G. A. and Oatman, E. R. (1982), Biology of *Trichogramma brevicapillum*. *Entomol. Exp. Appl.*, **32**, 61-67.
- Pak, G. A.; van Halder, I.; Lindeboom, R. and Stroet, J. J. G. (1985), Ovarian egg supply, female age and plant spacing as factors influencing searching activity in the egg parasite *Trichogramma* sp. *Med. Fac. Lanbouww. Rijksuniv. Gent.*, **50**, 369-378.
- Reznick, D. (1985), Costs of reproduction: an evaluation of the empirical evidence. *Oikos*, **44**, 257-267.

- Salt, G. (1934), Experimental studies in insect parasitism. II. Superparasitism. *Proc. Roy. Soc. London B*, **114**, 455-476.
- Salt, G. (1940), Experimental studies in insect parasitism. VII. The effect of different hosts on the parasite *Trichogramma evanescens* Westw. (Hym.: Chalcidoidea). *Proc. Roy. Soc. London A*, **15**, 81-124.
- Shorey, M. H. and Hale, R. H. (1965), Mass rearing of the larvae of nine noctuid species on a simple artificial medium. *J. Econ. Entomol.*, **58**, 522-524.
- Smith, S. M.; Hubbes, M. and Carrow, J. R. (1986), Factors affecting inundative releases of *Trichogramma minutum* Ril. against the spruce budworm. *J. Appl. Entomol.*, **101**, 29-39.
- Smith, S. M. (1996), Biological control with *Trichogramma*: Advances, successes, and potential of their use. *Annu. Rev. Entomol.*, **41**, 375-406.
- Statistical Analysis Systems Institute, Inc. (1994), User's guide: Statistics. 6th ed. Cary, NC : SAS Institute Inc. 1686 pp.
- Stearns, S. C. (1992), The evolution of life histories. Oxford : Oxford University Press. 262 pp.
- Trudeau, D. and Gordon, D. M. (1989), Factors determining the functional response of the parasitoid *Venturia canescens*. *Entomol. Exp. Appl.*, **50**, 3-6.
- Volkoff, A. N. and Daumal, J. (1994), Ovarian cycle in immature and adult stages of *Trichogramma caccoeciae* and *T. brassicae* (Hym.: Trichogrammatidae). *Entomophaga*, **39**, 303-312.
- Waage, J. K. and Ng, S. M. (1984), The reproductive strategy of the parasitic wasp. I. Optimal progeny and sex allocation in *Trichogramma evanescens*. *J. Anim. Ecol.*, **53**, 401-415.
- Yu, D. S. K.; Hangley, E. A. C. and Laing, J. E. (1984), Biology of *Trichogramma minutum* Riley collected from apples in southern Ontario. *Env. Entomol.*, **13**, 1324-1329.
- Zar, J. H. (1984), Biostatistical Analysis. 2nd ed. Englewood Cliffs : Prentice-Hall. 718 pp.

Received: August 21, 2002;

Revised: May 06, 2003;

Accepted: August 11, 2003.