EFFECT OF HOST AVAILABILITY ON *Trichogramma cordubensis* (INSECTA: HYMENOPTERA) REPRODUCTIVE STRATEGIES

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The effect of host availability on *Trichogramma cordubensis* Vargas & Cabello (Hymenoptera, Trichogrammatidae) fecundity and survival rates was analysed in this study. When hosts were daily provided (either with an unlimited or limited number), wasps had the highest rate of reproduction in the first day of parasitism, decreasing with oscillating values thereafter. When a limited number of hosts was provided with 3 days intervals, the parasitoids reproduction rate was significantly reduced, tending to be equally distributed throughout lifetime. A positive linear relation was found between reproduction and survival: wasps that had daily oviposited had greater longevity than those that had oviposited only every 3 days or did not oviposit. These results suggest that *T. cordubensis* is able to adjust fecundity schedule as an adaptation to changing hosts resources, which is an important survival feature for this species as host shortage is likely to occur in nature.

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INTRODUCTION

Numerous parasitoids are efficient natural enemies of important agricultural and forestry pests, and among these, the genus *Trichogramma* Westwood is worldwide used in several pest management programs (LI-YING 1994). *Trichogramma* are minute wasps that oviposit into the eggs of other insects, and depend upon these hosts as food resources for their larvae. According to several authors the lifetime reproductive success of the wasp increases as progeny number allocated to the host decreases (KLOMP & TEERINK 1978; PAK & OATMAN 1982; WAAGE & LANE 1984; WAJNBERG et al. 1989; NENON 1993). Therefore, to allocate the progeny suitably, these wasps must respond to the number of host eggs locally available, by ovipositing few eggs per host if the probability of finding enough hosts is high. Optimal strategies for exploiting host resources are essential for survival of the species and their usefulness as biological control agents. However, the role of host availability on the reproductive success of *Trichogramma* species has been poorly investigated despite its importance in natural biotopes and biological control programs (SCHMIDT & SMITH 1985; BAI & SMITH 1993; FLEURY & BOULÉTREAU 1993; MANICKAVASAGAM et al. 1994).

Trichogramma cordubensis Vargas & Cabello (Hymenoptera, Trichogrammatidae) is a native species for the island of São Miguel (Azores) (PINTUREAU et al. 1991). The evaluation of the effectiveness of this species as a biological control agent for agricultural pests existing in the Azores islands has been investigated in our laboratory, by studying the parasitoid biology (PINTO & TAVARES 1991; GARCIA & TAVARES 1995, 1997), population dynamics (GARCIA et al. 1995) and rearing techniques (TAVARES & VIEIRA 1992). As part of this research, the evaluation of the effect of host availability on *T. cordubensis* fecundity and survival rates was analysed in this study.

MATERIAL AND METHODS

T. cordubensis was obtained from parasitized eggs of *Autographa gamma* Linnaeus (Lepidoptera, Noctuidae), collected at Ribeira do Guilherme (São Miguel island). Parasitoid laboratory rearing was made on eggs of the host *Ephestia kuehniella* Zeller (Lepidoptera, Pyralidae) according to the methods of TAVARES & VIEIRA (1992).

In the experiments, eggs of *E. kuehniella* were presented to parasitoids as egg cards that were prepared by mixing one surface of a rectangular piece of index card with a water solution of non-toxic glue, and then spreading the required number of host eggs on this surface. A drop of honey was poured on the surface of the egg card to provide the parasitoids a carbohydrate source. The host eggs were less than 24 hours old and had been previously ultra-violet irradiated for 20 minutes.

To test the effect of host availability on the fecundity and longevity of *T. cordubensis*, the following four treatment groups were assembled: group A (n = 33 females), each female was provided, per day, with a host unlimited egg card (i.e., with 140 ± 8 eggs per egg card); group B (n = 32 females), each female was provided, per day, a host limited egg card (i.e., 10 eggs per egg card); group C (n = 31 females), each female was provided, every 3-day intervals, a host limited egg card (i.e., 10 eggs per egg card); group D (n = 31 females), no host eggs were available for each female. For all treatment groups, each egg card was exposed to the female wasp only during 24 hours. Females from group C were deprived of hosts during the first three days of their lives, therefore the first supply of hosts was only given on day 4. The experiments ran in temperature cabinets at 20 ± 0.5 °C, 75 ± 5 % R.H. and L:D 16:8 h. Cards with parasitized eggs were maintained under the same conditions for wasp progeny development. Wasp fecundity was determined by counting the number of parasitized host eggs (weather parasitoids emerged or not), since the eggs of *E. kuehniella* are relatively small and *Trichogramma* females always oviposit only one wasp per host egg. However, adult offspring was counted to check the any occurrence of superparasitized eggs. The number of parasitized hosts was determined by counting the host eggs that turned black, using a dissecting microscope at 25X. Egg chorions of insects infested by *Trichogramma* turn black when parasitoids are in the prepupal stage. This is caused by black deposits that forms a cocoon-shaped cuticle around the body of the larva and inner surface of the chorion of the host egg (SAAKIAN-BARANOVA 1991). Longevity was determined by checking the number of dead parental females once a day, starting from the day of their adult emergence. Wasps who drowned in the honey were eliminated from the statistical analysis.

Fecundity and longevity comparisons between different treatment groups were performed using an analysis of variance (ANOVA). When statistical differences existed between data sets, a Sheffé test was made to separate the differing means. Fecundity data was transformed by $\sqrt{(x+0.5)}$ to reduce variance differences (ZAR 1996). A regression between lifetime fecundity and longevity data was calculated.

RESULTS

For all treatment groups only one parasitoid emerged from each host egg, indicating the absence of superparasitism.

When hosts were daily supplied, the greatest progeny production (mean ± s.e.) was observed on the first day for group A (12.9 ± 2.2 parasitized eggs per female), and the first and second days for group B (7.1 ± 1.2 and 7.5 ± 1.3 parasitized eggs per female, respectively), sharply decreasing with oscillating values thereafter on both treatment groups (Fig. 1). However, fecundity for the first day was significantly higher (ANOVA, $F=14.527$, $df=2$ & 102, $P<0.0001$) in host unlimited (group A) than in both host limited treatments (groups B and C). The mean (± s.e.) fecundity of parasitoids from group C (host limited with 3-day intervals) was inferior on the first day of parasitism (4 ± 0.7 parasitized eggs per female), but afterward was almost equally distributed throughout female's lifetime. In this group, wasps parasitized almost the totality of available hosts during their existence, except for parasitoids with expanded longevity. For these last, fecundity decreased after the 21st day probably due to depletion of female's egg supply (Fig. 1).

Mean (± s.e.) lifetime fecundity of each female was significantly higher (ANOVA, F=34.570, df=2 & 102, P <0.0001) when hosts were daily supplied in unlimited (82.8 ± 6.3 parasitized eggs per female of group A) or limited (85.3 ± 6.5 parasitized eggs per female of group B) numbers, than when a limited number of hosts was provided with 3 day intervals (26.3 ± 2.9 parasitized eggs per female of group C) (Fig. 2).

Longevity did not differ significantly (Sheffé Test, P =0.9086) between wasps that were daily given host eggs (group A, mean ± s.e. = 22 ± 1.6 days; group B, mean ± s.e. = 23 ± 1.5 days). However, longevity was significantly higher (ANOVA, F=19.780, DF=3 & 123, P <0.0001) for parasitoids that had daily available hosts than those that did not (group C, mean ± s.e = 16 ± 1.1 days; group D, mean ± s.e. = 11 ± 0.7 days) (Fig. 2). A positive (rather than a negative) linear relation was found between the averages of longevity and lifetime fecundity of the wasps (F = 117.919, df = 1 & 94, P <0.0001, Fig. 3).

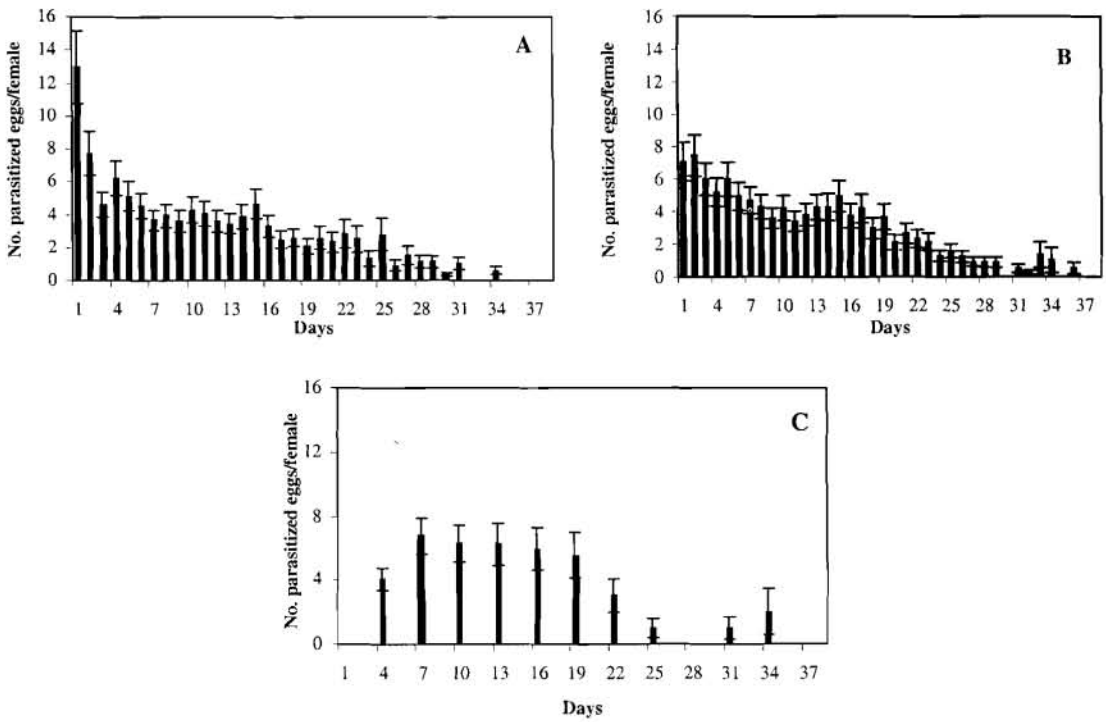

Fig. 1. Number (mean ± s.e.) of parasitized eggs per female of *T. cordubensis*, when daily provided with an unlimited (A) or limited (B) number of hosts, and supplied with a limited number of hosts every 3-day (C).

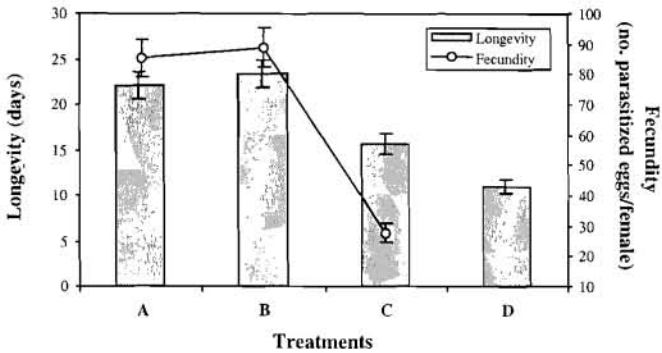

Fig. 2. Longevity (mean ± s.e.) and lifetime fecundity (mean ± s.e.) of *T. cordubensis* females, when daily provided with an unlimited (A) or limited (B) number of hosts, and supplied with a limited number of hosts every 3-day (C).

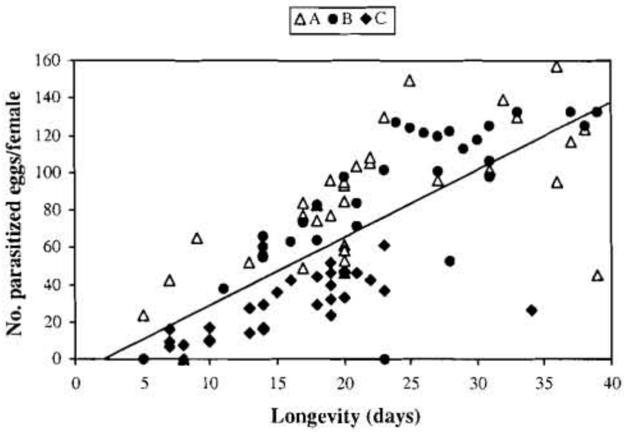

Fig. 3. Relationship of the total number of parasitized eggs per wasp with longevity; $y = -6.224+3.622x$, $r^2 = 0.556$, $P < 0.0001$.

DISCUSSION

Our results show that the longevity of the wasps was influenced by host availability: wasps that had daily-oviposited (provided daily with hosts) had greater longevity than those that had oviposited only every 3 day or did not oviposit. Adult feeding by the parasitoids on a carbohydrate source increases longevity and fecundity (CABELLO GARCIA & VARGAS PIQUERAS 1985; HOMANN et al. 1989; LAETEMIA et al. 1995). In our experiments all the parasitoids had access to honey as a carbohydrate source. *Trichogramma* has been observed to feed on hosts occasionally after oviposition (TAVARES 1985; MANWEILER 1986; HOMANN et al. 1988). This feeding behaviour allows the intake by the ovipositing wasp of food resources that exist in the host and are not available in honey. The daily consumption of such resources probably increased the wasp's longevity, as our results point out: wasps that were given hosts only every 3-day or lacking hosts available, had a shorter life span in spite of being fed with honey.

A positive linear relation was found between average longevity and lifetime fecundity: females that produced the greatest number of progeny also lived the longest, whereas those that did not produce any progeny had the shortest life span. BAI & SMITH (1993) also found a positive correlation between reproduction and survival of *Trichogramma minutum* Riley but they did not found evidence for a trade-off between wasps' fecundity and longevity. On the other hand, MANICKAVASAGAM et al. (1994) observed opposite relations between fecundity and longevity depending on the species: a negative correlation was observed for *Trichogramma pretiosum* Riley and a positive for *Trichogramma chilonis* Ishii.

Host availability influenced *T. cordubensis* lifetime fecundity: lifetime fecundity was higher when hosts were daily supplied. The reduction in the overall fecundity of the wasps without daily available hosts could result either from their shorter life spans (e.g., parasitoids with lower longevity have a shorter period to oviposit) or due to egg oosorption by the wasp. ANUNCIADA & VOEGELÉ (1982), by dissecting females of *Trichogramma brassicae* Bezdenko, observed that resorption of chorionated eggs occurred after 3 days of host deprivation. Later, FLEURY & BOULÉTREAU (1993) verified that *T. brassicae* parasitization capacity was drastically reduced due to egg resorption when parasitoids were submitted to host deprivation for 4 days. Oosorption is viewed as an adaptive strategy allowing females to conserve their metabolic resources instead of laying eggs under unfavourable conditions. Therefore, if oosorption occurs in *T. cordubensis* when wasps are deprived of hosts and is accompanied by reduction in overall fecundity, then it would be adaptive for this species only if other components of fitness are improved. Such components could be the dispersion of parasitization that would either enhance the avoidance of predation or hyperparasitization. FLEURY & BOULÉTREAU (1993) found that the dispersion of parasitization of *T. brassicae* increased when host deprivation exceeded one day.

Trichogramma is considered to be pro-ovigenic (oogenesis is completed prior to adult emergence), therefore females lay most of their eggs shortly after emergence (PAK & OATMAN 1982). However, WANG & SMITH (1996) and VOLKOFF & DAUMAL (1994) showed that thelytokous parasitoids are more similar to synivogenic wasps because they carry few mature eggs in their ovaries at emergence and display a steady pattern of ovarian development. We verified that *T. cordubensis* (a thelytokous wasp) had the highest fecundity on the first day when hosts were daily offered in unlimited or limited numbers, dropping with oscillating values in the subsequent days. If the ovipositing female could count the total number of hosts locally available, then its optimal strategy would be to partition progeny over all available hosts, therefore increasing the fitness of each offspring by reducing the stress of predation and hyperparasitization. However, "host counting" is not possible, so when hosts are available the wasp exploits them as much as possible during the first few days of adult life. Moreover, according to our results when hosts are unavailable for some days, females are able to compensate the reduction in fecundity by dispersing the ovipositions more equally throughout their life, parasitizing most of the hosts they are able to find. These results suggest that *T. cordubensis* is able to adjust fecundity schedule as an adaptation to changing host's resources, which is an important survival feature for this species as host shortage is likely to occur in nature.

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