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Abstract

Trichogramma are facultative gregarious egg parasitoids that attack a wide range of lepidopterous eggs. Because hosts in which parasitoids develop vary in terms of available food, the progeny produced by parasitoid females vary in size and fitness. While one might expect that the developmental rate and emergence rhythm should be similar for all individuals reared under the same environmental conditions, variations in the duration of development of individuals reared under uniform conditions have been found in several insect species. In the Hymenopteran egg parasitoid *Trichogramma evanescens* Westwood (Hymenoptera: Trichogrammatidae) adults emerge at the beginning of the photoperiod on two consecutive days. Longer development may influence the fitness of adults and have an impact on mating opportunities. Size, longevity and daily and lifetime fecundity were measured for female *T. evanescens* that developed in nine and ten days. We observed a significant relationship between size and both longevity and lifetime fecundity. While early emerging females did not live longer and did not produce progeny with a different sex-ratio than females that emerged later, they were larger and produced more progeny than late females. We conclude that early emerging females have a higher fitness than late emerging females *T. evanescens*.

Keywords: emergence, fecundity, longevity, parasitoid, sex-ratio, size

Introduction

Trichogramma species are facultatively gregarious (Rabinovich 1971), polyphagous egg parasitoids that are often used in inundative biological control programs (Smith 1996) against a wide range of Lepidopterous eggs (Corrigan and Laing 1994). *Trichogramma* spp. are moderately synovigenic (Jervis et al. 2001) and females start to lay their eggs shortly after emergence (Bigler et al. 1987; Chassain and Boulétreau 1991). Hosts in which parasitoids develop are variable resources in terms of available food and, as a result, parasitoid adults vary in size with males being generally smaller than females (van den Assem et al. 1989). In a host of a given size, females grow larger than males and males emerge earlier than females (Charnov et al. 1981).

Several studies have found that the female's fitness increases with its size (King 1987; Boivin and Lagacé 1999) indicating that, for an adult parasitoid, being large has consequences on its reproductive success (van den Assem et al. 1989). While body size has no direct relation to fitness, it may be used as a primary proxy when its relationship with another primary proxy (for example fecundity, longevity or mating ability) is known (Roitberg et al. 2001). The size of a female may influence its longevity, its searching efficiency, its egg load and its capacity to locate hosts. The size of a male may influence its longevity, its capacity to locate females and the number of matings (Godfray 1994). In general, the size of *Trichogramma* species seems to be positively related to performance (McDougall and Mills 1997).

Insect developmental rates and emergence rhythms tend to be similar for all individuals of a population reared under the same environmental conditions (Saunders 1976; Beck 1991). However, variations in the developmental period of cohorts reared under the same conditions have been found in many insects (Shaffer 1983). In the species *Trichogramma evanescens*, emergence occur mostly at the beginning of the photoperiod and are spread over two days (nine and ten days at 24 ± 1 °C) with 89% of the males and 95% of the females emerging on the first day (Doyon and Boivin 2004). Because emergence is concentrated at the beginning of the photoperiod, the duration of immature development varies by a few hours between individuals depending on the time of egg deposition. When a female parasitizes a host late in the day, the immature may not be ready to emerge on the morning of the ninth day and have to delay its emergence until the next day. Individuals that delay emergence may experience either an increase or a decrease in fitness, depending on how host resources are used. An increase in fitness is expected if the supplementary developmental time can be used by the individual to either exploit more fully the host resource or to mature. However, a decrease in fitness is more likely if the individual is merely waiting for emergence while burning reserves to maintain its somatic functions. Individuals emerging later can also be penalized by encountering low-quality mates (Carvalho et al. 1998) or by experiencing lower mating opportunities (Waage and Ng 1984).

Emerging early in the day is certainly an advantage for short-lived diurnal species such as *Trichogramma*. Under laboratory conditions, *T. evanescens* females deposit 56% of their eggs during

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the first 24 hours (Boivin and Lagacé 1999) and survival in the field probably does not exceed 24–48 hours. It is, therefore, important to emerge at the beginning of a day when host location is possible. Females that are unable to emerge on the morning of the ninth day are thus facing a trade-off between emerging late in the day and missing oviposition opportunities or delaying emergence to the tenth day and possibly having a lower fitness.

In this paper, we compared the longevity, fecundity (daily and lifetime fecundity) and size of females *T. evanescens* that emerged after nine days of development (early females) versus females that emerged after ten days of development (late females).

Material and Methods

Biological material

The *T. evanescens* strain we used originated from Egypt, and was reared on *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs at 25 ± 1 °C, $40 \pm 10\%$ RH under a light dark photoperiod of 8L:16D. Individuals of *E. kuehniella* were reared at 25 ± 2 °C, $40 \pm 10\%$ RH and 8L:16D. The *E. kuehniella* eggs were less than 24 h old and were cold sterilized at −15 °C for 24 h.

Longevity, fecundity and size of female T. evanescens

Approximately 100 *T. evanescens* females were placed in contact with about 1000 *E. kuehniella* eggs for 30 min and after which the eggs were incubated at 24 ± 1 °C. Under these conditions, female *T. evanescens* emerge on the ninth (early females) and tenth (late females) days after oviposition (Doyon 2004). Early (n = 29) and late females (n = 26) were individually mated at emergence by a male less than 3 h old and were then placed in a 3.7 ml tube (without food) with approximately 250 eggs of *E. kuehniella* that were changed every 24 h during the life of the female. These eggs were incubated in the same rearing chamber, in 3.7 ml tubes, and at emergence the individuals were counted and the sex-ratio calculated. To determine the longevity of early (n = 30) and late females (n = 30), we monitored their survival every 4 h (±15 min) from 6:30 to 22:30. The death of females was assigned to the mid-point between two observations. Because overall body size and hind tibia length are highly correlated in *Trichogramma* species (Bai 1986), and because it is less sensitive to distortion than other body parts (Bai 1986), at the end of the experiment, the hind tibia length of all female *T. evanescens* was measured.

Statistical analyses

Linear regressions were used to obtain the relation between size and longevity, and size and lifetime fecundity. An analysis of covariance with size as co-variable was used to compare the lifetime fecundity of early and late females. The longevity and daily fecundity of early and late females *T. evanescens* were compared with *t*-tests. The Fisher's exact test was used to compare the daily sex-ratio of the progeny of the females.

Results

As expected, a significant relationship was found between size and longevity (Fig. 1) and size and lifetime fecundity (Fig. 2) for both early and late females. The mean longevity of early females

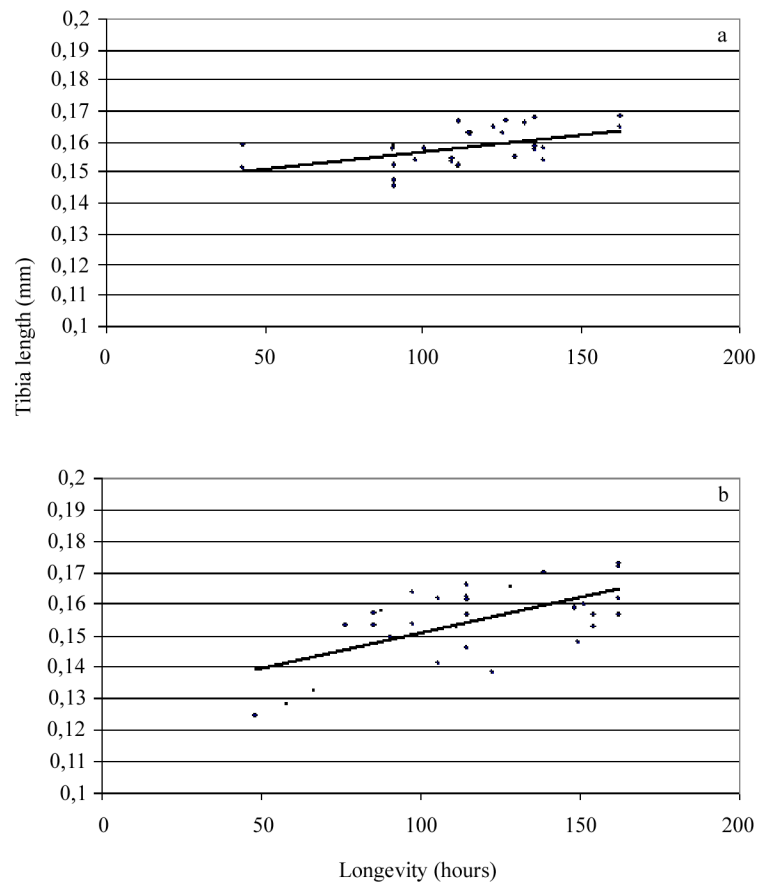**Figure 1.** Longevity vs. tibia length of (a) early females (linear regression R = 0.516, d.f. = 29, *p* d" 0.01). (b) late females (linear regression R = 0.624, d.f. = 29, *p* d" 0.01).
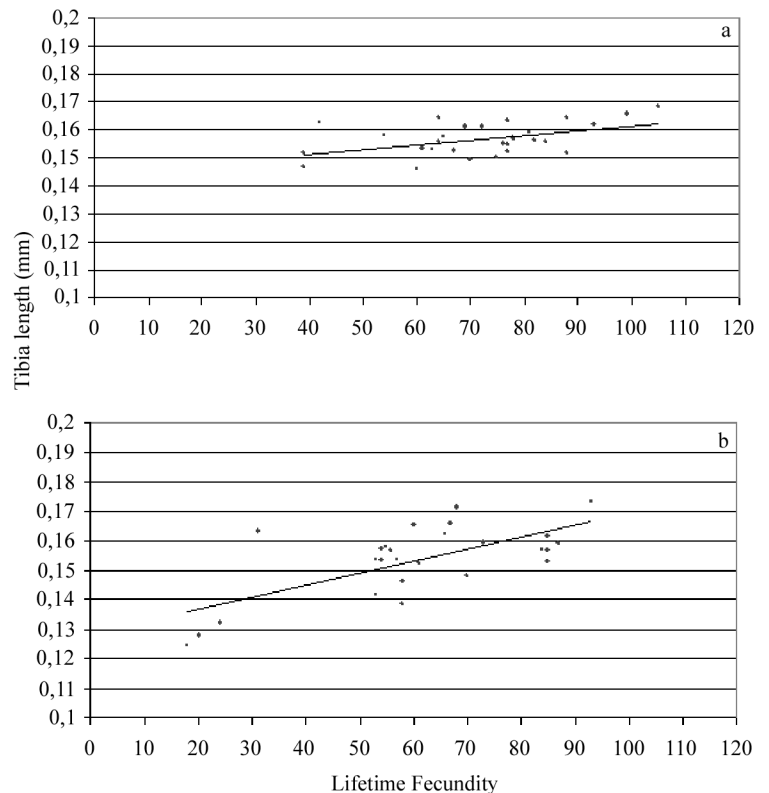

Figure 2. Lifetime fecundity vs. tibia length of (a) early females (linear regression R = 0.478, d.f. = 28, p d" 0.01). (b) late females (linear regression R = 0.676, d.f. = 25, p d" 0.01).

Table 1. Daily fecundity of early and late female *T. evanescens* reared on *E. kuehniella*.

Day	Daily fecundity of early females (±SD)	Daily fecundity of late females (±SD)	t-test
1	35.10 ± 5.17	29.38 ± 7.19	t= 4.14 df= 53 p = 0.01
2	12.59 ± 3.18	10.80 ± 3.46	t= 2.21 df= 52 p = 0.034
3	11.56 ± 3.98	9.60 ± 3.80	t= 2.35 df= 50 p = 0.025
4	7.41 ± 3.15	5.85 ± 3.01	t= 2.30 df= 45 p = 0.029
5	7.84 ± 4.24	6.21 ± 3.57	t=2.04 df= 31 p = 0.057
6	4.86 ± 2.39	7.60 ± 3.44	t= -1.65 df= 10 p = 0.166
7	4.50 ± 1.17	4.83 ± 2.44	t= -2.05 df= 6 p = 0.922

Table 2. Sex-ratio of early and late females *T. evanescens* reared on *E. kuehniella*.

Source	df	Sum of square	Mean square	F value	Pr > F
Model	2	8157.24	4078.62	18.84	< 0.0001
Error	52	11260.15	216.54		
Corrected total	54	19417.38			
Size	1	7386.93	7386.93	34.11	< 0.0001
Lifetime fecundity	1	770.3	770.3	3.56	0.0649

Table 3. Analysis of variance of the lifetime fecundity of early and late females with size as a co-variable.

Source	df	Sum of square	Mean square	F value	Pr > F
Model	2	8157.24	4078.62	18.84	< 0.0001
Error	52	11260.15	216.54		
Corrected total	54	19417.38			
Size	1	7386.93	7386.93	34.11	< 0.0001
Lifetime fecundity	1	770.3	770.3	3.56	0.0649

(112.45 ± 0.25 h) was not significantly different from the longevity of late females (116.25 ± 0.25 h) (t = –0.0164; df = 58; p = 0.630). The longevities varied from a minimum of 43.5 h to a maximum of 162.5 h.

On the first four days of their life, early females had a higher daily fecundity than late females. From day 5 to day 7, there was no significant difference between the fecundity of early and late females (Table 1). The daily (Table 2) and lifetime sex-ratio of the progeny produced by early and late females did not differ (Fisher's exact test p = 0.4284; df = 1; p > 0.05). However, the sex-ratio of the progeny of females increased with the age of the female in both treatments (Table 2).

Because fecundity is correlated with size in many parasitoid species, the lifetime fecundity of females was analyzed with size as a co-variable. While the complete model showed highly significant differences between durations of development, the individual analysis indicated that lifetime fecundity showed no significant differences, although fecundity was higher for females with short developmental time (early females = 70.18 eggs, late females = 62.57 eggs). Size was highly significantly correlated with fecundity (Table 3). The mean hind tibia length was 0.160 ± 0.007 mm for early females and 0.154 ± 0.012 mm for late females. The smallest hind tibia length was 0.141 mm for early females and 0.124 mm for late females.

The largest hind tibia length was 0.178 mm for early females and 0.173 (±0.012) mm for late females.

Discussion

In *T. evanescens*, a significant relationship was found between the size of females and both longevity and lifetime fecundity. These data confirm the results of Waage and Ng (1984), van den Assem (1989), Bennett and Hoffmann (1998), Boivin and Lagacé (1999), Sagarra et al. (2001) and Rivero and West (2002) who showed that large females parasitoids live longer and produce more progeny than small females, and therefore are at an advantage because they have a higher fitness. Therefore, if differences in size are observed between early and late females, we can predict that these differences will translate into differences in fitness.

Both longevity and the sex-ratio of progeny oviposited by early and late females did not vary significantly. In parasitic Hymenoptera, progeny sex-ratios are known to vary and to be determined at oviposition by arrhenotoky (Luck et al. 1992) where males develop from unfertilized eggs (haploid) and females from fertilized eggs (diploid) (Flanders 1965). Following mating, female parasitoids store sperm and can manipulate the sex-ratio of their progeny by controlling the access of sperm to the egg during

oviposition (Flanders 1965; Suzuki et al. 1984). The gradual increase in sex-ratio that was observed was due to sperm depletion of the female (Boivin and Lagacé 1999, Boivin et al. 2004). Female *T. evanescens* can store up to 50 sperm in their spermatheca (Damiens unpublished data).

Early females were larger and more fecund than late females and they produced 18.8% more progeny. Because each egg deposited contributes to the reproductive success of females, early females had a higher fitness than late females. Thus, emerging early had a considerable effect on the size of females and their production of eggs. Although the effect of emergence day on fecundity was almost significant, most of that effect was due to the difference in size between early and late females. The late females were probably not ready to emerge at the beginning of the photoperiod on day 9, so they had to wait another 24 hours to emerge as adults. This increase in developmental time as pupae or sub-imago could have used part of their energy reserves which resulted in a smaller size and a lower fecundity. In *Trichogramma* parasitoids, oogenesis starts during the pre-pupal stage (Volkoff and Daumal 1994) and continues after adult emergence (Mills and Kuhlmann 2000). *Trichogramma* species have been reported as proovigenic by several authors (Pak and Oatman 1982; Waage and Ng 1984; Bai et al. 1992) but they have since been described as moderately synovigenic (Jervis et al. 2001). In many species, females emerge with an egg load that accounts for a fraction of their potential fecundity (Houseweart et al. 1983; Smith and Hubbes 1986; Bai and Smith 1993; Kuhlmann and Mills 1999). Our hypothesis was that females would spend some of their resources maintaining their somatic functions while waiting for emergence on the tenth day. However, exhausting resources, probably of their fat reserve, should not have influenced the size of the females when measured as hind tibia length. The results suggest that it was not the longer developmental time that produced small individuals but rather that the smaller individuals took longer to develop.

Superparasitism, which is of common occurrence in *Trichogramma* spp. in the laboratory (Yadav et al. 2001), could also be the cause of the increase in developmental time in late females. The eggs of *E. kuehniella* usually support the development of a single adult *Trichogramma* per egg. However, more than one parasitoid egg may be initially deposited per host (Klomp and Terrink 1978). Larval competition results in the death of some individuals and the survival of others (Corrigan et al. 1995). Superparasitism affects subsequent parasitoid development (Ahmad et al. 2002) and has been suggested as a factor leading to extended emergence periods in several *Trichogramma* species (Parra et al. 1988).

Trichogramma spp. are the most widely used parasitoid agents for the biological control of lepidopterous pests (Waage and Ng 1984). They are particularly used in inundative releases projects (Corrigan and Laing 1994). The negative impact of longer development on the size and fecundity of *Trichogramma* females suggests that the quality of the individuals produced in mass rearing could be improved by maximizing the proportion of the population emerging early.

Acknowlegements

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