Effect of host availability on reproduction and survival of the parasitoid wasp *Trichogramma minutum*

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Abstract. 1. We tested the hypothesis that females of the egg parasitoid, *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae), could adjust their fecundity schedule according to host availability and that there was a negative correlation between reproduction and survival in these wasps.

2. Newly-emerged females were provided with an unlimited or limited number of hosts in the first trial and with either unlimited, limited or zero hosts in the second trial.

3. When hosts were unlimited, wasps had the highest rate of reproduction in the first day, which decreased dramatically thereafter. When hosts were limited, wasps from the two trials differed in their response. In Trial I, females with limited hosts had lower first-day fecundity than, and the same subsequent-day fecundity as, those with unlimited hosts. However, in Trial II, females with limited host had a lower first-day but a higher subsequent-day fecundity than those with unlimited hosts. This indicates variation in *Trichogramma*'s ability to shift its fecundity schedule in response to host availability.

4. There was a positive (rather than a negative) correlation between reproduction and survival. Wasps that oviposited (in host-unlimited treatment) had greater longevity than those that could not (in host-unavailable treatment).

5. The sex ratio of the progeny produced by wasps in both host-unlimited and limited treatments shifted gradually from a female to a male bias as the wasps aged.

6. We consider the ability of parasitoids to adjust their fecundity schedule as an adaptation to changing host resources and discuss our findings with regard to theories of life history evolution.

Key words. Reproduction, survival, life history, *Trichogramma minutum*, fecundity schedule, longevity, parasitoid, sex ratio.

Introduction

The hypothesis of tradeoffs between life history characters states that there exists a negative correlation between major components of fitness in organisms due to the constraints on the rate at which resources can be acquired and used for vital functions (Reznick, 1985; Bell & Koufopanou, 1986). These tradeoffs are most often expressed as a negative correlation between early and late reproduction (Charlesworth, 1980; Luckinbill *et al.*, 1987) or between reproduction and survival (Roitberg, 1989). The life history hypothesis has been approached theoretically from perspectives of both evolutionary optimization and quantitative genetics (Charlesworth, 1990) and has been tested experimentally from both perspectives in many organisms (Reznick, 1985; Partridge & Barton, 1993). Empirical evidence from these tests generally supports the notion that an increase in early reproduction or in fecundity causes a decrease in late reproduction or in longevity. However, this hypothesis has rarely been tested empirically in one group of animals, i.e. parasitic Hymenoptera (but see Mackauer, 1982; Kopelman & Chabora, 1992), although a considerable amount of theoretical work on parasitoid oviposition decisions (e.g. Charnov & Stephens, 1988; Mangel, 1989; Godfray & Parker, 1991) assumed tradeoffs in life history characters. Considering the significance of many parasitic species as biological control agents for suppressing pests, it is important to test and verify the validity of the hypothesis in this

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group. We present herein a test in parasitoids employing the optimization approach. The results may have potential application in biological control programmes in which a known tradeoff may be manipulated to either prolong females' longevity or promote their reproduction to achieve a better level of pest control.

Many insect parasitoids are beneficial to humans and are used against various pests in agriculture, forestry and public health (Clausen *et al.*, 1977). Whether in their natural habitat or in inundative biological control programmes (where large numbers of parasitoids are released in the field to control pests), some parasitoids will find hosts immediately or soon after they emerge or are released in the field, while others will not. Also some individuals may find hosts on one day but not on other days, and others may never find hosts during their life. Such variation in host finding is likely to be common in the field where the spatial or temporal distribution of hosts changes. The question then arises: can parasitoids adapt to host availability in the environment? Specifically, do parasitoids lose their fecundity for the day that they do not find hosts or do they compensate by laying more eggs when they find hosts in the future?

Previous work on fecundity and host utilization in two species of hymenopterous parasitoids, *Aphelinus semiflavus* and *Leptopilina boulardi*, suggested that females could shift their fecundity schedule according to host density (Mackauer, 1982) or host availability (Kopelman & Chabora, 1992) although the experiments were not specifically designed to test the tradeoff between early and late reproduction. We were interested in testing the ability of parasitoids to adjust their fecundity schedule as a modification of the hypothesis on tradeoffs between early and late reproduction. We wanted to know whether limited host availability forced parasitoids to spread their oviposition relatively evenly throughout their adult life span, i.e. whether the reduction in their early, natural oviposition peak due to host shortage could be compensated for by an elevation or a delayed decrease in oviposition during later stages.

We were also interested in testing tradeoffs between fecundity and longevity in parasitoids. The theory states that organisms have to partition their investments between gametic production and somatic maintenance and repair (Kirkwood, 1981; Roff, 1984). The more investments go to gametic production, the less will be available to somatic maintenance and vice versa. For a parasitoid, this means that if she invests more in reproduction and lays many eggs, she will have relatively less to invest in maintenance and repair, i.e. to prolong her longevity. Therefore she is more likely to die before her counterpart who does not invest as much in reproduction. On the contrary, if she produces few eggs, she will have more resources left to invest in her somatic maintenance. Thus, she might live longer than a female who invests more in reproduction.

The egg parasitoid, *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae), is commonly distributed in North American forests and parasitizes a number of forest pests including the spruce budworm

(*Choristoneura fumiferana*) (Anderson & Kaya, 1976; Sanders *et al.*, 1985). During an outbreak of spruce budworm, natural populations of *Trichogramma* are not large enough to suppress the pest population. Therefore a biological control programme using inundative releases of *T.minutum* to suppress budworm in Canadian forests has been tried and shows some promising results (Smith *et al.*, 1990). We have chosen the parasitoid *T.minutum* as our model system to test the hypotheses of fecundity schedule adjustment and tradeoffs between fecundity and longevity for two reasons. First, this species, like many other species of *Trichogramma*, is synovigenic. Females emerge with a complement of eggs which account for only a fraction of their total egg production in a lifetime (Houseweart *et al.*, 1983; Smith & Hubbes, 1986; B. Bai, unpublished). Wasps continue to mature eggs throughout their adult life although egg production during the first few days is grnerally much greater than that during late adult life. Our unpublished data also suggest that females of this species can absorb eggs when starved, and thus reallocate resources into different functions, possibly from reproduction to survival. Second, in the field, this species is likely to encounter a situation similar to that which the hypotheses postulate, i.e. a foraging parasitoid may not find hosts for some period or find hosts sporadically and therefore face the problem of tradeoffs. We report our test results in *T.minutum* on tradeoffs between (1) early and late reproduction and (2) reproduction and survival. We discuss our findings with regard to the theory of life history evolution.

Materials and Methods

Insect cultures and general methods

The experimental animal, *T.minutum*, was collected in July 1988 from five parasitized spruce budworm egg mases on balsam fir near Quetico Park, Ontario, Canada (48.7° N 91.1° W). The parasitoids were maintained in the laboratory on eggs of the Angoumois grain moth, *Sitotroga cerealella* Olivier (Lepidoptera: Gelechiidae) until 1990 and then switched to the Mediterranean flour moth, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) until completion of the experiments. Our rearing hosts, *S.cerealella* and *E.kuehniella*, were obtained from cultures maintained in the Biological Control Laboratory, Department of Environmental Biology, University of Guelph, Ontario, Canada. All experiments were conducted and parasitoid colonies were maintained under laboratory conditions at $25 \pm 1°C$, 16L:8D and 65–85% r.h.

In the experiments, eggs of *E.kuehniella* were presented to parasitoids in the form of egg cards which were prepared by misting one surface of a rectangular piece of index card (0.5×3.0 cm) with water and then spreading the required number of host eggs on this surface. Eggs of *Ephestia kuehniella* have a water-soluble mucous substance on the outside of their chorion which adheres to the wet surface of the cards. Each host egg could also be gently removed without damage by using a fine brush that was wetted on

the tip. After exposure to the parasitoids, half the host eggs (in Trial I, see below) were removed and dissected in a drop of water on a microscope slide under a dissecting microscope to determine if and how many parasitoid eggs were deposited.

Experimental design

To test the hypothesis that female parasitoids can adjust their fecundity schedule according to host availability and tradeoff longevity with reproduction, we designed the following experiments where the parasitoids' fecundity and longevity were measured under different conditions of host availability.

Two-group treatment (Trial I). Newly-emerged, mated females (≤6 h old) from the same cohort were randomly assigned to one of two treatment groups: host unlimited and host limited. Wasps in the first group (*n* = 20 females) were each provided in a glass vial (1.0 cm diameter by 3.5 cm height) with an egg card that had about eighty eggs of *E.kuehniella* attached, whereas those in the second group (*n* = 20 females) were singly provided with an egg card that had only fourteen host eggs. In both groups, egg cards were replaced daily so that females had fresh hosts available to them each day. Because a preliminary experiment showed that females in their first couple of days following emergence had the highest rate of oviposition, which subsequently decreased (average forty eggs in the first day, twenty eggs in the second day and about ten or less eggs per day thereafter), we used a stepped decrease in host numbers in the host-unlimited treatment, i.e. we provided eighty host eggs to each female daily for the first 3 days followed by sixty eggs daily for the next 3 days and twenty eggs per day thereafter until her death. Because *T.minutum* normally develops solitarily in eggs of *E.kuehniella*, this sheme provided unlimited hosts to a parasitoid throughout her life while reducing unnecessary dissections in the subsequent counting of parasitoid eggs. For the host-limited treatment, we provided fourteen host eggs to each female daily until her death.

A streak of diluted honey was replenished on the inside wall of the vial every other day to provide the parasitoids with a carbohydrate source. Parasitized egg cards from each day in each treatment were cut in half. Eggs on one half were dissected to count the number of parasitoid eggs laid in each host (to detect possible superparasitism) whereas those on the other half were returned to a growth chamber for incubation and emergence of parasitoid progeny. For both groups the information was collected on the number of hosts parasitized and the number of eggs laid per female per day (from dissection), the number of progeny emerged and their corresponding sex ratio (from emergence). We also recorded each (parental) females' longevity.

Three-group treatment (Trial II). The experiment was repeated as above with the addition of a host unavailable treatment. This addition extended the variation of host availability to the extreme, from host-unlimited to host-

unavailable. The host-unlimited treatment was the same as before except this time we did not dissect any exposed hosts but let all the parasitoid progeny emerge. Because the previous experiment showed little superparasitism and low mortality of immature parasitoids when hosts were unlimited, we could determine accurately how many parasitoid eggs were laid by counting the number of emerging progeny.

The host-limited treatment was modified. Each parasitoid was provided with twenty fresh host eggs at 3-day intervals (e.g. a female was given twenty eggs on day 1, 4, 7, 10, 13, 16, . . ., each for 24 h, but not on the other days). For a foraging *Trichogramma*, this pattern of host limitation may approximate the field situation better, especially in inundative release programmes, than the previous design where fourteen hosts were provided every day. In the field, it is unlikely that a parasitoid can find suitable hosts continuously each and every day during its entire life. The chance that a parasitoid finds a suitable host generally decreases with the relative abundance of parasitoids versus hosts, which can be high in certain times and locations or in biocontrol programmes where large numbers of parasitoids are released. The above pattern of host finding is better represented by the periodic (rather than continuous) host provisioning in this treatment. After exposure to the parasitoids, half of the hosts were again dissected whereas the other half were left in the growth chamber for emergence of parasitoid progeny.

Females in the host-unavailable treatment were given only diluted honey (with no host eggs) every other day like those in the other treatments. Longevity of each female was recorded. This was to test whether non-reproduction by parasitoids could prolong their longevity, i.e. whether fecundity had a tradeoff relationship to longevity.

Statistical analysis

For the treatments where we cut half of the exposed host egg card for dissection and left the other half for emergence, we calculated daily fecundity of each female in different treatment groups by adding the number of hosts parasitized in that day (from dissection) and the number of progeny produced in the same day (from emergence). Comparisons of fecundity between different treatment groups were analysed using a one-way analysis of variance, and emergence rate was compared using a χ^2 statistic (Sokal & Rohlf, 1981). We used Proc Lifetest in the Survival Analysis section of an IBM PC version of the SAS computer package (SAS, 1990) to analyse our longevity data.

Results

When hosts were unlimited, female *T.minutum* produced a large proportion of their progeny during the first few days, especially in the first 3 days during which wasps realized about 50% of their total life-time fecundity (Fig. 1). Off-
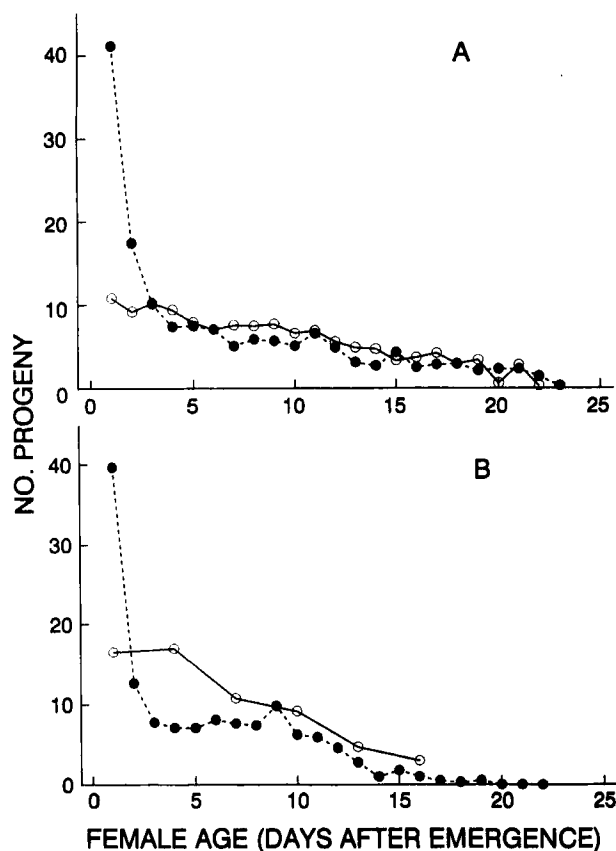
Fig. 1. Age-specific fecundity of female *Trichogramma minutum* provided with an unlimited (solid circles) and a limited (open circles) number of hosts, *Ephestia kuehniella* eggs. (A) Trial I. (B) Trial II.

spring prodiction was greatest in the first day of adult life and then decreased dramatically. In Trial I (Fig. 1A), the cumulative fecundity for the first 3 days of adult life was lower for females in host-limited (mean $\pm$SE = 29.7 $\pm$ 1.2) than in host-unlimited (mean $\pm$SE = 69.7 $\pm$ 3.2) treatment (one-way Anova, F = 141.71; df = 1, 35; P = 0.0001), but the subsequent-day fecundity was the same for the two treatment groups (mean $\pm$SE = 79.2 $\pm$ 9.1 and 68.8 $\pm$ 5.1; one-way Anova, F = 0.96; df = 1, 35; P = 0.333). In Trial II (Fig. 1B), although patterns in the first day fecundity between the two treatment groups agreed with those found in Trial I (host limited, mean $\pm$SE = 17.4 $\pm$ 0.8; host unlimited, mean $\pm$SE = 40.1 $\pm$ 1.8; one-way Anova, F = 130.0; df = 1, 36; P = 0.0001), those of subsequent-day fecundity disagreed. Cumulative fecundity at day 4, 7, 10, ..., was higher for wasps in host-limited (mean $\pm$SE = 34.2 $\pm$ 3.6) than in host-unlimited (mean $\pm$SE = 22.4 $\pm$ 2.7) treatment (one-way Anova, F = 6.64; df = 1, 36; P = 0.014). Further analysis showed that the life-time fecundity of females from the host-limited treatment (mean $\pm$SE = 51.5 $\pm$ 4.0) did not differ from the cumulative fecundity of their counterparts from the host-unlimited treatment (mean $\pm$SE = 60.9 $\pm$ 3.0) at the corresponding age, i.e. fecundity at age 1, 4, 7, 10, ... days (Fig. 1B;

one-way Anova, F = 3.60; df = 1,37; P = 0.066). Note that the absolute life-time fecundity from the two treatment groups in Trial II were not directly comparable due to the difference in exposure times — one group was exposed to host each and every day, the other only at certain days.

Superparasitism, i.e. laying more than one egg in a single host by females, was common for the first 3 days in Trial I (Fig. 2, 28.6%, 12.9% and 6.2% for day 1, 2, 3, respectively) and became sporadic thereafter (not shown) when hosts were limited. This contrasted to almost zero superparasitism for the same time period (1.4%, 0%, 0%, respectively) when hosts were unlimited. A high degree of superparasitism was also observed in the host-limited treatment of our second experiment (Trial II, 28.6%, 12.3% and 2.3% for day 1, 4, 7, respectively, Fig. not shown).

Parasitoid progeny had a higher non-emergence rate when hosts were limited than when they were unlimited (33/1039 versus 10/1552, χ^2 = 24.44, $P < 0.01$, Trial I). This corresponds qualitatively with the difference in superparasitism between the two treatments and indicates
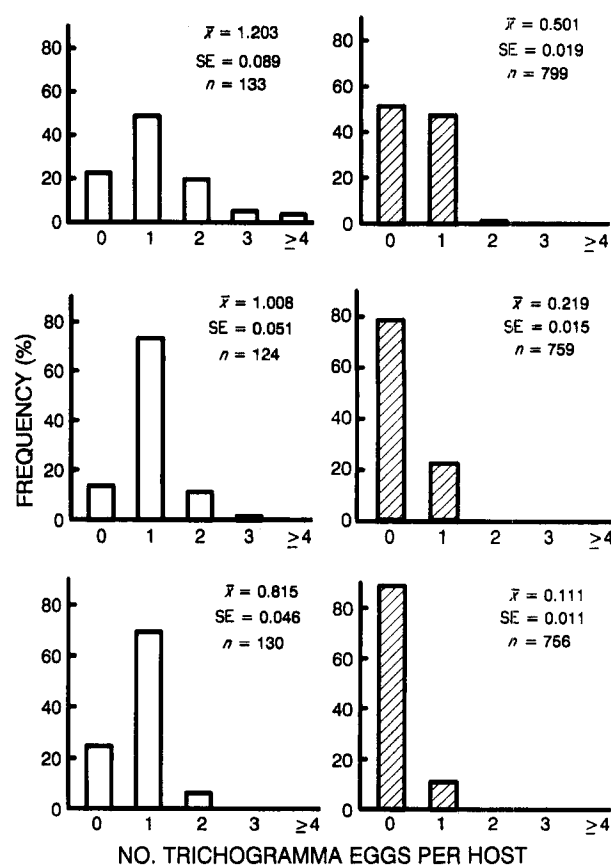

Fig. 2. Frequency distribution of hosts, *Ephestia kuehniella* eggs, that contain a different number of *Trichogramma minutum* eggs for host-limited (open bars) and host-unlimited (hatched bars) treatments. The figure shows the degree of superparasitism for the first 3 days under the two treatments. Top panel, day 1; middle panel, day 2; bottom panel, day 3. For all the panels, $\bar{x}$ = mean, SE = standard error, n = sample size.

that superparasitism may contribute to failure of emergence. We dissected parasitized hosts that lacked an emergence hole and found wasps had died inside the pupa as preadults.

Longevity did not differ between female parasitoids that had access to either an unlimited or limited number of hosts (for Trial I, mean longevity ±SE: 16.3 ± 1.4 versus 15.4 ± 1.3 days, log-rank test, $\chi^2 = 0.862$, $P = 0.353$, Fig. 3A; for Trial II, 13.5 ± 1.1 versus 11.0 ± 1.1, log-rank test, $\chi^2 = 2.558$, $P = 0.110$, Fig. 3B). However, the difference in longevity between the two extremes, host-unlimited and host-unavailable (mean longevity ±SE: 10.2 ± 0.8 days). was significant (log-rank test, $\chi^2 = 11.117$, $P = 0.0009$, (Fig. 3B). Parasitoids that could not oviposit did not live as long as those that laid all of their eggs.

The sex ratio of the progeny generally increased with the parental female's age (Fig. 4). There were three distinct phases in *T.minutum* sex allocation patterns at the population level. Young females (≤ 7 days old) produced a female-biased sex ratio ($<40\%$) whereas older ones (≥ 17 days old) allocated exclusively males. Between these extremes, wasps produced a gradually increasing sex ratio. These patterns held for females in both treatment groups.
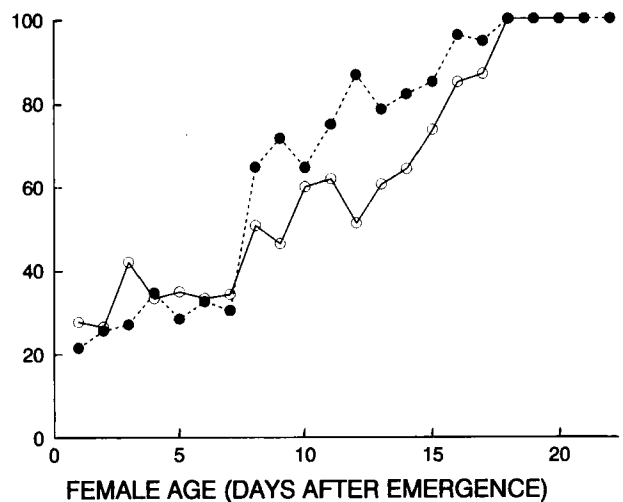
PROGENY SEX RATIO (% MALES)

Fig. 4. Daily sex ratio (% males) of the progeny produced by female *Trichogramma minutum* provided with an unlimited (solid circles) and a limited (open circles) number of hosts, *Ephestia kuehniella* eggs. The figure shows results from Trial I.
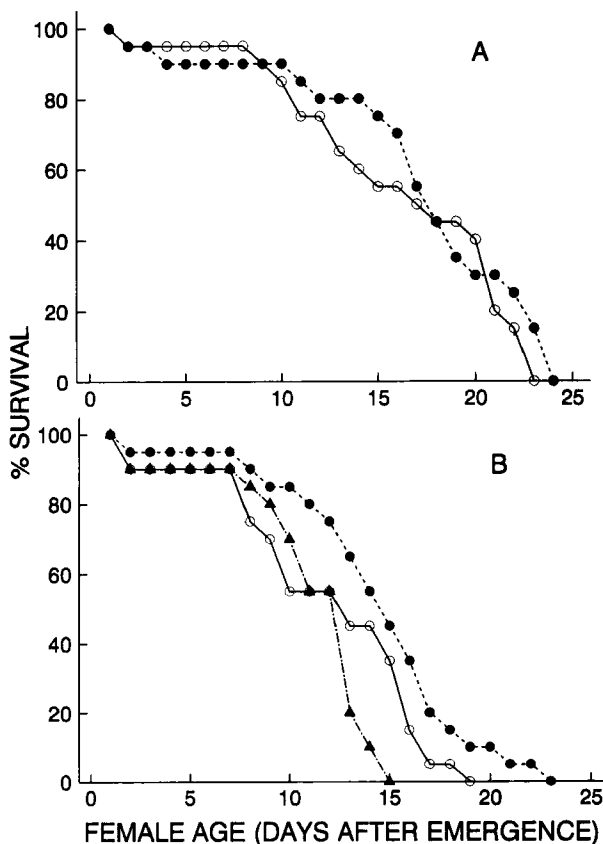

Fig. 3. Age-specific survival of female *Trichogramma minutum* provided with an unlimited (solid circles) and a limited number of hosts (open circles), *Ephestia kuehniella* eggs. (A) Trial I. (B) Trial II. Note the addition of the host-unavailable treatment (triangles) in this trial.

Discussion

Theories of life history evolution predict tradeoffs between life history characters in which an improvement in some fitness-related parameters is associated with a decrease in some other fitness-related parameters (Reznick, 1985). The most commonly referred tradeoffs are between early and late reproduction (Charlesworth, 1980) and between reproduction and survival (Daly, 1978; Roitberg, 1989). Two main theoretical models have been employed in the study of life history evolution. Optimization models do not contain specific genetic parameters, but assume that natural selection will lead to the establishment of a life history that maximizes fitness, within the intrinsic constraints of physiology and the extrinsic constraints of the environment. Genetic models, on the other hand, go a step further and examine whether a tradeoff is due to negative genetic correlation or mutation (Partridge & Barton, 1993). Using the egg parasitoid, *T.minutum*, as our model organism, we approached the question of tradeoffs in life history traits by experimentally manipulating allocation of resources in wasps to different traits, i.e. early versus late oviposition and reproduction versus survival. This is an alternative to genetic approach and conforms to the optimization analysis. As argued by some authors, this approach may provide the best strategy for determining patterns of tradeoffs (Bell & Koufopanou, 1986; Partridge & Harvey, 1988). We started out with a hypothesis that *Trichogramma* can adjust their fecundity schedule according to host availability and that there is a tradeoff between longevity and fecundity. Our results show that when hosts were limited, a female's first day or first few days' reproduction was restricted by host availability and the number of offspring produced was lower

than when hosts were unlimited. However, this early reduction in fecundity was compensated for by a relatively slow decrease in daily reproduction thereafter (Fig. 1) in Trial II but not in Trial I. This means that females in Trial II could shift their fecundity schedule in response to host shortage, i.e. a pattern of heavily skewed concentration of ovipositions at early adult stages was changed to that of relatively even distribution of ovipositions throughout adult life. Thus, wasps compensated for the early loss in fecundity by an adjustment of reproductive schedule. However, females in Trial I could not adjust their fecundity schedule and the early fecundity loss was not compensated for during late stages.

The difference between wasps in their ability to tradeoff early and late reproduction in the two trials could be attributed to the difference in experimental designs which represent field situations to different degrees. Wasps in Trial I had limited hosts available each and every day during their entire life whereas those in Trial II had access to limited hosts during only one third of their adult life time. Works on other parasitoid species also showed adjustment of reproduction by females in response to temporal host limitations (Drost & Carde, 1992; Kopelman & Chabora, 1992).

Our results also show that, given the opportunity, *T.minutum* will exploit its hosts as much as possible during the first day or first few days of adult life. When hosts are not available for some periods, females will be able to adapt by adjusting their fecundity schedule and thus compensating for the reduction in fecundity. In the field, host availability varies temporally and spatially. In the early or late season or during non-outbreak years, there are few spruce budworm eggs available and the parasitoids must search for alternative hosts (Houseweart *et al.*, 1984). In years of spruce budworm outbreaks there may be plenty of hosts available; however, budworm eggs in the field are only susceptible to parasitoid attack during the first 5 days from oviposition, after which embryos develop to advanced stages and eggs start to hatch (Houseweart *et al.*, 1982). Also, there may be geographical pockets or microhabitats with relatively low populations of spruce budworm. These factors point to a potentially unstable, changing environment for *Trichogramma*. A female wasp foraging in the field may or may not find hosts during certain periods of its adult life. Females will likely optimize their fitness if they can adapt to such an environment, i.e. exploit maximally when conditions are optimal and adjust fecundity schedule when conditions change.

Our results also offer some additional information which can be useful for the field application of *T.minutum* against the spruce budworm. In biological control programmes against the budworm, parasitoids are often released as preadults (parasitoids still in their pupal case but ready to emerge) during peak budworm oviposition. Given the expected variation in host availability in the field, some of these parasitoids will probably end up not finding hosts for some time. Therefore, promotion of their survival in the field, for example by providing a food source for emerging parasitoids, becomes one of the

important aspects to consider. These parasitoids can still cause a 'compensated' mortality to the hosts if they can find hosts again later.

Although a negative correlation between reproduction and survival was expected (Reznick, 1985; Bell & Koufopanou, 1986) and also supported by evidence from some other parasitoid species (e.g. Hohmann *et al.*, 1989; Orr & Boethel, 1990), we found a positive relationship between these two life-history parameters in *T.minutum*. Females that produced the greatest number of progeny also lived the longest whereas those that did not produce any progeny had the shortest lifespan (Fig. 3). There was no evidence that a tradeoff existed between longevity and fecundity in our trials. Available reports on the tradeoff between reproductive effort and survival in other organisms have been largely anecdotal and have shown mixed results, being negative in some animals (e.g. Roitberg, 1989) and neutral or positive in others (van Balen *et al.*, 1987; Moller *et al.*, 1989). In a model of resource acquisition and allocation (van Noordwijk & de Jong, 1986; de Jong & van Noordwijk, 1992), it was shown that depending on the relative variation in acquisition and allocation fraction, one could obtain either positive or negative phenotypic correlations between life history traits. Work on other arthropods (Calow, 1973; Browne, 1982) indicates that the negative effect of reproduction on survival is often more obvious when experimental animals are subjected to stressful conditions (e.g. scarcity of resources) than when they are under optimal conditions (e.g. abundance of resources or food). When conditions are optimal, negative correlations between fecundity and longevity sometimes become less clear or disappear. This is probably because the organisms can take up enough resources from the environment to replace the energy drain due to reproduction (Bell & Koufopanou, 1986). In our experiment, parasitoids in both treatments (host-unlimited and host-unavailable) had access to a food source, i.e. diluted honey. This food source might have contributed to the neutral and positive correlations that we found in *T.minutum*. Although *Trichogramma* spp. have been observed to feed on hosts occasionally after oviposition, available evidence indicates that host-feeding alone does not prolong longevity but honey-feeding alone does (e.g. Bai *et al.*, 1992). This was also true for *T.minutum* when we tested the effect of honey and host feeding on longevity, in a separate experiment, by assigning wasps from the same cohort into the following four groups ($n = 12$ wasps per group): (1) no host + no honey (longevity, mean $\pm$SE $= 1.0 \pm 0.0$ days a), (2) no host + honey (11.2 ± 1.8 b), (3) host + no honey (1.9 ± 0.3 a), (4) host + honey (8.6 ± 2.3 b) (longevity means followed by the same letters are not significantly different at 5% level, df $= 44$, Tukey's studentized range test).

Age-specific patterns of sex allocation by *T.minutum* were not influenced by host availability in our experiments (Fig. 4). Whether hosts were unlimited or limited, wasps always produced a female-biased sex ratio at early ages and almost exclusively males at the end of their life. Parasitic Hymenoptera normally copulate soon after their emergence. Females store sperm in their spermathecae

and decide whether or not to fertilize an egg when it is laid, thus directly controlling their progeny's gender (Flanders, 1956). We have not come across any references that show host availability affects parasitoid sex allocation or that sex ratio, as a fitness parameter, can be traded off with other fitness parameters such as fecundity or longevity although sex ratio can change with clutch size allocated to a specific host (Waage & Godfray, 1985).

Our experiments demonstrate a phenotypic correlation between early and late fecundity and between fecundity and longevity for parasitic Hymenoptera. As pointed out by Reznick (1985) and Partridge & Barton (1993), however, further demonstration of this relationship from the level of quantitative genetics will make our conclusion most convincing. Although the fecundity schedule adjustment as shown in *T.minutum* in Trial II supports the tradeoff hypothesis, results from Trial I and the positive correlation between reproduction and survival do not. Tests with more species of parasitoids are needed in order to draw any general conclusions about the validity of the hypothesis in parasitic Hymenoptera.

Acknowledgments

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