

EFFECTS OF ADULT NUTRITION ON LONGEVITY, FECUNDITY, AND OFFSPRING SEX RATIO OF *TRICHOGRAMMA MINUTUM* RILEY (HYMENOPTERA: TRICHOGRAMMATIDAE)

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Abstract

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The role of adult nutrition in longevity, progeny production, and offspring sex ratio of *Trichogramma minutum* Riley was examined. On average, honey-fed females lived 26.4 days and produced 260 offspring; unfed females lived 3.5 days and produced 80 offspring. Feeding on fructose or sucrose also significantly increased longevity and fecundity over unfed females (fructose, 23 days and 230 offspring; sucrose, 21 days and 230 offspring) but to a lesser degree than feeding on pure honey. Females fed yeast suspension or water had no significant increases in longevity or fecundity compared to unfed females. Offspring sex ratios of long-lived females were male-biased (50–62% males), those of short-lived females were female-biased (74–82% females). Lifetime reproduction of honey-fed females was highest at 20–25°C and relative humidities of 20–80%, but short-term offspring production (during the first 2 days after emergence) was highest at 30°C and 60–80% RH. Females that had access to honey for only a 24-h period did not increase their offspring production over the first 4 days of their lives when compared to unfed females. The potential benefits of feeding adult *T. minutum* for mass-rearing and field release are discussed.

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Résumé

Nous avons étudié l'influence de l'alimentation des adultes sur la longévité, la fécondité et le rapport mâles:femelles de la progéniture chez *Trichogramma minutum* Riley. En moyenne, les femelles nourries de miel ont vécu 26,4 jours et produit 260 rejetons; les femelles non nourries ont vécu 3,5 jours et produit 80 rejetons. Les femelles nourries de fructose ou de sucrose avaient également une longévité accrue et une plus grande fécondité que les femelles non nourries (fructose, 23 jours et 230 rejetons; sucrose 21 jours et 230 rejetons), mais l'effet de l'alimentation était moindre que chez les femelles nourries de miel pur. L'alimentation des femelles au moyen de suspensions de levures ou d'eau n'a augmenté ni la longévité, ni la fécondité. Le rapport mâles:femelles de la progéniture des femelles à longévité élevée était supérieur à 1 (50–62% de mâles), celui de la progéniture des femelles à longévité courte, inférieur à 1 (74–82% de femelles). La fécondité totale des femelles nourries de miel était maximale à 20–25°C, à une humidité relative de 20–80%, mais la fécondité maximale à court terme (au cours des 2 premiers jours après l'émergence) a été observée à 30°C, à une humidité relative de 60–80%. Les femelles qui n'ont eu accès à du miel que pour une période de 24 h n'ont pas connu d'amélioration de leur fécondité pendant les 4 premiers jours de leur vie. Les avantages reliés à l'alimentation des adultes de *T. minutum* au cours des programmes d'élevage en masse et de libération en nature font l'objet d'une discussion.

[Traduit par la Rédaction]

Introduction

The efficacy of the polyphagous egg-parasitoid, *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae), in suppressing populations of the spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), has been assessed in a mass-rearing and inundative release program (Smith et al. 1990). Parasitism of over 80% was recorded from the field, but this level of parasitism required the release of high numbers (19–28 × 10⁶) of females per hectare (Smith et al. 1990). In commenting on the potential of

T. minutum to be commercially viable in competition with current control strategies, Carrow et al. (1990) stressed the need to reduce the costs per parasitoid in the mass-rearing system and to improve the quality of the parasitoids to reduce the numbers required for a release.

Several authors have determined that feeding the adults of several *Trichogramma* species greatly increased their longevity, vigour, and fecundity in the laboratory (List and Davis 1932; Lund 1938; Narayanan and Mookherjee 1956; Ashley and Gonzales 1974; Hohmann et al. 1988). Yu et al. (1984) demonstrated that feeding honey to female *T. minutum* increased their fecundity 6-fold and their longevity 9-fold over unfed wasps. Potentially, by allowing the adult parasitoids to feed, both mass production and field efficacy of *T. minutum* could be greatly improved by relatively simple means.

In these studies, we compared unfed adults to those fed with various carbohydrate sources or a protein source for adult longevity and fecundity and the sex ratio of their offspring. To identify the environmental conditions that would maximize the benefits of adult feeding, fed and unfed parasitoids were examined at various temperatures and relative humidities. As well, the parameters described above were measured for unfed adults and adults that were allowed to feed for only 24 h to estimate the potential effect of feeding adults, before release, on their subsequent performance in the field.

Materials and Methods

The Host. Eggs of the Mediterranean flour moth, *Ephestia kuehniella* (Zeller), were used as hosts for *T. minutum* throughout all experiments. They were obtained from a laboratory colony maintained in the Biological Control Laboratory, Department of Environmental Biology, University of Guelph. Eggs of *E. kuehniella* were sterilized with gamma radiation (approximately 60 krad), then stored at 2°C for no more than 8 days before they were used in our experiments.

The Parasitoid. The *T. minutum* used in this study were originally collected from eggs of the spruce budworm in Quetico Park, Ontario (S.M. Smith, pers. comm.), and had been in continuous culture for about 20 generations. Cultures were maintained by exposing approximately 80 000 eggs of *E. kuehniella* on a glass plate to approximately 10 000 adult female wasps for 24 h in a 30- by 30- by 40-cm parasitization box (Laing and Eden 1990). Parasitized eggs were placed in 37.5-mL glass vials and kept at $25 \pm 0.5^\circ\text{C}$, $50 \pm 5\%$ RH, and 16L:8D photoperiod until the wasp progeny emerged (ca. 9–11 days after parasitism).

General Experimental Methods. Female parasitoids used in all experiments were taken from batches of newly emerged adults (<12 h old) in the 37.5-mL vials; mating was assumed to have taken place in the vials. Over many experiments, we have found the frequency of unmated females (based on their production of exclusively male offspring) to be less than 3% (Corrigan and Laing, unpublished). The newly emerged, female *T. minutum* were placed individually in 3-mL glass vials and were offered eggs of *E. kuehniella* on sample strips made of 3M Post-it® message pads; each strip held about 175 host eggs (Corrigan and Laing 1991). The strips were changed every 2 days until the parasitoids died. Longevity of each female was recorded by daily visual checks for parasitoid mortality. For each sample strip, the number of host eggs parasitized (blackened eggs) was counted 5 days after exposure of the strip to a parasitoid. Superparasitism was not considered to be a factor because, in situations of ready host availability, female *Trichogramma* produce a single offspring per host in eggs of *E. kuehniella* (Salt 1940; Bigler et al. 1987). The lifetime production of each parasitoid was obtained by totalling the parasitized eggs from all strips. After the F₁ adults emerged, they were killed by freezing at -15°C to stop them producing an F₂ generation on the same strip, then their numbers and gender were recorded. Unless otherwise specified, adult parasitoids had access to their particular nutrient throughout their lives; and all experiments were conducted at $25 \pm 0.5^\circ\text{C}$, $50 \pm 5\%$ RH, and 16L:8D photoperiod. In all

experiments, 30 females were started per treatment. Sample sizes shown in the results reflected loss of parasitoids that got stuck in the nutrients or were lost during handling and were not the result of natural mortality. Voucher specimens of *T. minutum* used in the experiments have been deposited in the insect collection at the University of Guelph.

Effect of Types and Concentrations of Food. Female *T. minutum*, held individually in 3-mL vials, either were not fed or were given one of the following: water, undiluted unpasteurized honey, an aqueous solution of either 50% unpasteurized honey, 20% sucrose, 50% sucrose, 20% D-fructose, or 50% D-fructose, or an aqueous suspension of 20% or 50% brewers yeast. Concentrations of food solutions available during the adult's lifespan were calculated by weight and presented as small droplets (less than 2 mm in diameter) inside the vials. Water, 20% yeast, and 50% yeast suspensions were presented in absorbent cotton and were replenished every 2 days.

To determine the effects of the types and concentrations of food listed above on the longevity of male *T. minutum*, the experimental technique was identical to that used for females, except that the yeast suspensions were presented as small droplets inside the vials.

We conducted preliminary trials in which all nutrients were presented in cotton; we had a problem with the parasitoids becoming trapped in the cotton balls containing carbohydrate solutions. It was thought not possible to deposit a droplet of water or yeast suspension large enough to prevent evaporation between monitoring sessions and small enough to prevent the droplet from rolling around inside the vials and trapping the parasitoids. Because of the greater viscosity of the carbohydrate solutions, fluid movement in the vials was not a problem for these treatments. We conducted the experiment on food types and male longevity at some time after the experiment was done with the females. By that time, we knew that the yeast suspensions could be presented in the same manner as the carbohydrate solutions with no greater risk of evaporation or trapping the parasitoids. Water was always presented in small cotton balls. Preliminary experiments indicated that there were no differences in longevity of males and females or fecundity of females exposed to carbohydrate solutions in droplets or in cotton (Leatemia, unpublished).

Effect of Temperature. Female parasitoids either not fed or fed with a drop of undiluted honey were held individually in 3-mL vials in environmental cabinets at 16, 20, 25, or 30°C with a 16L:8D photoperiod. Parasitoids remained under these conditions, except for daily exposure to room temperature (about 21°C) for less than 20 min per day to check for parasitoid mortality, and to change the supply of host eggs every 2nd day. After exposure to parasitoids, the sample egg strips were kept at $25 \pm 0.5^\circ\text{C}$, $50 \pm 5\%$ RH, and 16L:8D photoperiod until the adult progeny emerged.

Effect of Relative Humidity. For each treatment, newly emerged, female *T. minutum* were held in 3-mL glass vials with screen mesh tops to allow the humidity to equilibrate inside and outside the vials. The parasitoids were either not fed or fed with a drop of undiluted honey and were placed in plastic, non-vacuum desiccators, sealed with grease and "O" rings, in which relative humidity was maintained at 20, 40, 60, or 80% by aqueous solutions of potassium hydroxide (Buxton 1931). While we observed parasitoid mortality and changed host eggs, the parasitoids were exposed to room conditions for less than 20 min per day. Host eggs, which had been exposed to parasitoids, were kept at $25 \pm 0.5^\circ\text{C}$, $50 \pm 5\%$ RH, and 16L:8D photoperiod until the adult progeny emerged.

Effect of Limited Feeding. Females were left unfed, or they were fed with a drop of undiluted honey for the first 24 h after emergence, for 24 h beginning 48 h after emergence, or for the entire experimental period. Offspring production was measured as the number of blackened eggs produced per female parasitoid during the first 4 days after eclosion, because it was felt that this was a better reflection of potential activity in the field than was lifetime offspring production. All female parasitoids used in the analyses lived for at least 4 days.

Data Analysis. Data were subjected to analysis of variance using the general linear model (GLM) procedures of SAS (SAS Institute 1985). Differences between treatment means were analyzed using the least significant difference test (SAS Institute 1985). An arcsin transformation was employed on proportional data (sex ratio) prior to GLM analyses (SAS Institute 1985).

Results

Effect of Types and Concentrations of Food. When provided with 100% honey, adult female *T. minutum*, held at 25°C, 50% RH, and 16L:8D photoperiod, lived significantly longer than unfed females or those provided with any other nutrient except 20% fructose or 50% honey (Table 1). The other carbohydrate sources (sucrose and 50% fructose), although not increasing longevity as much as 100% honey, resulted in females that lived approximately 6 times as long as unfed females (Table 1). Providing females with water or yeast suspension did not significantly increase longevity over those females that were not fed. The concentration of the respective nutrients did not significantly affect longevity (Table 1).

The longevity of male *T. minutum* was not significantly different among those individuals with access to any of the carbohydrate sources, but individuals in these treatments lived significantly longer than males without access to food or males with access to yeast or water (Table 1). The longevity of males fed non-carbohydrate sources was not significantly different among themselves (Table 1).

Female *T. minutum* given honey increased their lifetime offspring production approximately 3-fold compared with unfed parasitoids (260 versus 80 offspring per female, Table 2). Access to sucrose or fructose allowed females to produce approximately 230 offspring, significantly more than unfed females but significantly less than those females with access to 50% honey (Table 2). There were no significant differences in lifetime production among females fed yeast or water or females that were not fed. The concentrations of each nutrient had no significant effect on offspring production (Table 2).

Yeast-fed, water-fed, and unfed parasitoids lived, on average, for less than 4 days and produced 52.7–66.4 offspring during the first 2 days of adult life (Table 2). Honey-fed and sugar-fed females produced similar numbers of offspring in the first 2 days (range 57.8–68.7 offspring per female, Table 2) but lived for many more days, producing moderate numbers of offspring per day until their death (Fig. 1).

TABLE 1. Longevity of adult *Trichogramma minutum* given different types and concentrations of food at 25 ± 0.5°C, 50 ± 5% RH, and 16L:8D photoperiod

Treatment	Number observed	Females		Males	
		\bar{x} (days) ± SD	Number observed	\bar{x} (days) ± SD	
100% honey	25	26.4 ± 6.6 a*	22	6.1 ± 2.3 a	
50% honey	24	25.7 ± 6.2 ab	26	5.4 ± 1.5 a	
50% fructose	28	22.7 ± 8.4 bcd	27	5.9 ± 1.7 a	
20% fructose	26	23.8 ± 8.8 abc	26	5.9 ± 1.6 a	
50% sucrose	30	21.7 ± 4.9 cd	26	5.4 ± 1.6 a	
20% sucrose	26	20.6 ± 6.2 d	26	5.4 ± 2.1 a	
50% yeast	25	2.6 ± 1.0 e	29	1.3 ± 0.4 b	
20% yeast	29	2.5 ± 0.6 e	27	1.1 ± 0.3 b	
Water	20	2.4 ± 0.8 e	30	1.8 ± 0.2 b	
Unfed	22	3.5 ± 0.8 e	30	1.1 ± 0.3 b	

*Means followed by the same letter in a column are not significantly different at the 5% level by least significant difference test.

TABLE 2. Lifetime offspring production of *Trichogramma minutum*, offspring production during the first 2 days of oviposition, and percentage female progeny of parasitoids given different types and concentrations of food at $25 \pm 0.5^\circ\text{C}$, $50 \pm 5\%$ RH, and 16L:8D photoperiod

Treatment	Number observed	Offspring production \pm SD		% female progeny \pm SD
		Lifetime	First 2 days	
100% honey	25	259.6 \pm 59.9 ab*	61.8 \pm 10.5 acd	38.2 \pm 16.8 a
50% honey	24	267.1 \pm 75.6 a	68.7 \pm 11.8 b	45.9 \pm 14.5 ab
50% fructose	28	227.4 \pm 63.0 c	64.4 \pm 8.0 abc	49.9 \pm 17.4 b
20% fructose	26	233.9 \pm 75.2 bc	58.9 \pm 9.0 cde	41.2 \pm 17.0 b
50% sucrose	30	227.1 \pm 61.1 c	61.7 \pm 14.9 acd	49.1 \pm 17.4 b
20% sucrose	26	232.0 \pm 50.1 bc	57.8 \pm 6.4 def	43.6 \pm 11.8 ab
50% yeast	25	55.4 \pm 14.0 d	53.3 \pm 11.4 ef	79.6 \pm 7.9 cd
20% yeast	29	54.4 \pm 12.4 d	52.7 \pm 11.2 f	74.2 \pm 10.4 c
Water	20	68.3 \pm 14.9 d	65.2 \pm 13.2 abc	83.9 \pm 4.6 d
Unfed	22	79.9 \pm 13.8 d	66.4 \pm 8.8 ab	81.8 \pm 6.6 cd

*Means followed by the same letter in a column are not significantly different at the 5% level by least significant difference test.

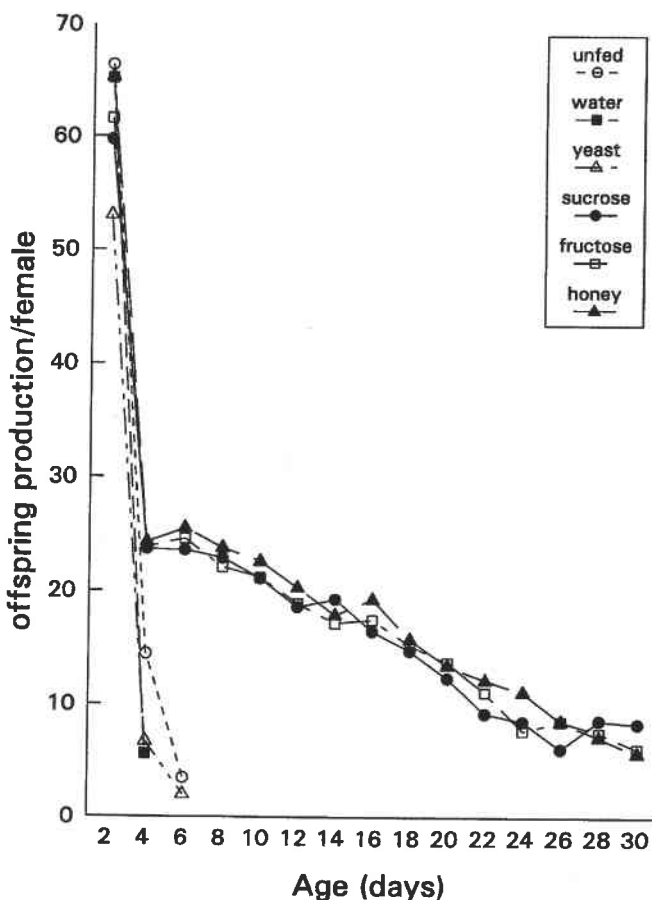


FIG. 1. Age-related offspring production by *Trichogramma minutum* given different feeding regimes.

TABLE 3. Longevity, lifetime offspring production, offspring production during the first 2 days of oviposition of *Trichogramma minutum*, and percentage female progeny of fed and unfed parasitoids held at various temperatures

Treatment	No. obs.	Longevity (days) \pm SD	Offspring production \pm SD		% female progeny \pm SD
			Lifetime	First 2 days	
Honey 16°C	24	44.7 \pm 17.2 a*	205.5 \pm 64.5 a	51.9 \pm 7.4 a	55.7 \pm 16.9 a
Honey 20°C	29	35.2 \pm 9.1 b	258.6 \pm 57.7 b	61.2 \pm 7.6 b	44.5 \pm 12.7 b
Honey 25°C	26	27.3 \pm 6.3 c	246.9 \pm 45.7 b	71.4 \pm 10.0 c	43.1 \pm 15.8 b
Honey 30°C	25	17.1 \pm 2.2 d	209.0 \pm 41.8 a	81.7 \pm 9.0 d	48.9 \pm 14.1 ab
Unfed 16°C	28	7.1 \pm 3.6 e	78.2 \pm 31.7 cd	49.2 \pm 16.6 a	80.5 \pm 10.8 c
Unfed 20°C	30	6.0 \pm 2.0 e	92.9 \pm 17.9 c	64.7 \pm 9.5 be	79.2 \pm 8.6 c
Unfed 25°C	29	3.7 \pm 1.4 ef	83.6 \pm 24.5 cd	68.3 \pm 15.9 ce	75.4 \pm 7.7 c
Unfed 30°C	28	1.8 \pm 0.6 f	65.7 \pm 14.3 d	65.2 \pm 13.5 bc	75.2 \pm 13.7 c

*Means followed by the same letter in a column are not significantly different at the 5% level by least significant difference test.

Honey-fed and sugar-fed parasitoids produced a significantly lower proportion of female progeny than unfed parasitoids and those given yeast or water (Table 2). This reduction occurred because, after 6 days of oviposition, increasing numbers of the females produced broods of exclusively male offspring (Leatemia et al. 1995).

Effect of Temperature. Longevity of honey-fed parasitoids decreased significantly as the temperatures at which the females were held increased from 16 to 30°C (Table 3). A similar, but less statistically significant, trend was found for unfed females. Lifetime offspring production for honey-fed females was significantly higher at 20 and 25°C than it was at 16 or 30°C (Table 3). Again, a similar trend was found for unfed females, but fewer significant differences existed among treatments than existed for honey-fed females. For honey-fed females, offspring production in the first 2 days increased with temperature and was significantly higher at 30°C than at any other temperature (Table 3). Unfed females showed no significant differences in offspring production in the first 2 days at any temperature above 16°C (Table 3). When compared at each temperature, honey-fed parasitoids lived 6–9 times longer than unfed females and produced 2.5–3 times more offspring during their lives, although the sex ratio of their offspring was significantly more male-biased than the respective unfed treatment (Table 3).

Effect of Relative Humidity. Longevity of honey-fed females was highest at 40% RH, and was significantly higher than longevity of females kept at 60% or 80% RH, but not significantly different from those females kept at 20% RH (Table 4). Longevity of unfed females was not significantly different at any of the relative humidities, but as in previous results, honey-fed females lived approximately 5 times longer than unfed females at the same relative humidity (Table 4). Lifetime offspring production was not affected in any discernible pattern by humidity within either the honey-fed or the unfed treatments (Table 4). Honey-fed treatments had approximately 2.5 times higher fecundities measured over a lifetime, but significantly more male-biased offspring sex ratios than their respective unfed counterparts (Table 4). For honey-fed females, offspring production during the first 2 days was significantly higher at 60% and 80% RH than it was at 20% or 40% RH (Table 4). There were no significant differences for this parameter among the unfed treatments.

Effect of Limited Feeding. Offspring production over the first 4 days by *T. minutum*, fed for the entire experimental period, was significantly higher (90.6 \pm 15.3 offspring, $N = 25$, $P < 0.05$, LSD test) than that of parasitoids fed for the first 24-h period of their lives (76.9 \pm 13.8 offspring, $N = 22$), those fed for 24 h, 2 days after emergence (82.3 \pm 10.2 offspring, $N = 24$), or those females that never fed (81.1 \pm 12.4 offspring, $N = 22$).

TABLE 4. Longevity, offspring production during the first 2 days of oviposition, lifetime offspring production of *Trichogramma minutum*, and percentage female progeny of fed and unfed parasitoids held at various relative humidities, $25 \pm 0.5^\circ\text{C}$, and 16L:8D photoperiod

Treatment	Number observed	Longevity (days) \pm SD	Offspring production \pm SD		% female progeny \pm SD
			Lifetime	First 2 days	
Honey 20% RH	27	26.5 \pm 5.4 ab*	229.6 \pm 57.1 a	59.8 \pm 10.6 a	51.0 \pm 15.2 a
Honey 40% RH	26	28.5 \pm 5.4 a	218.8 \pm 35.4 ab	59.7 \pm 9.4 a	50.7 \pm 15.2 a
Honey 60% RH	28	25.4 \pm 6.1 b	224.4 \pm 32.2 a	66.1 \pm 11.9 b	53.1 \pm 13.0 a
Honey 80% RH	25	20.7 \pm 6.1 c	205.0 \pm 41.9 b	65.1 \pm 10.7 b	56.2 \pm 12.8 a
Unfed 20% RH	30	5.4 \pm 1.9 d	83.7 \pm 30.8 c	56.1 \pm 6.0 a	75.0 \pm 12.4 b
Unfed 40% RH	30	5.0 \pm 1.7 d	79.4 \pm 30.9 c	59.2 \pm 8.8 a	69.4 \pm 17.6 b
Unfed 60% RH	30	4.8 \pm 1.1 d	81.2 \pm 23.9 c	58.8 \pm 9.6 a	74.6 \pm 7.9 b
Unfed 80% RH	30	4.4 \pm 1.1 d	75.1 \pm 20.8 c	59.8 \pm 8.3 a	67.8 \pm 16.9 b

*Means followed by the same letter in a column are not significantly different at the 5% level by least significant difference test.

Offspring production of parasitoids fed for a 24-h period, regardless of when that period occurred, was not significantly different from that of unfed parasitoids.

Discussion

In our experiments, female *T. minutum* fed on undiluted honey showed the maximum increases in longevity and lifetime fecundity over unfed parasitoids. Our data are very similar to those recorded for a population of *T. minutum* collected from eggs of the codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), that were fed honey and reared on eggs of *E. kuehniella* at 25°C (longevity 25.5 days; fecundity 236.8 eggs per female; Yu et al. 1984). The largest portion (85–95%) of the dry matter of honey consists of two sugars, fructose and glucose (White 1979). Females feeding on fructose and sucrose in our experiments lived longer and produced more offspring throughout their lives than unfed females, but their performance was slightly poorer than that of females fed undiluted honey. Narayanan and Mookherjee (1956) recorded significant increases in the longevity and fecundity of *T. evanescens* Westwood fed various sugars, but they did not report tests on honey-fed parasitoids. Carbohydrates apparently provide the parasitoids with a source of energy that allows them to live longer and produce more offspring, but there is some aspect of feeding on honey that is superior to refined sugars in increasing parasitoid quality with respect to reproduction. Because of this, we conducted all subsequent experiments with females fed undiluted honey versus unfed females.

Providing the parasitoids with yeast suspension did not increase longevity or lifetime fecundity of females over that recorded for unfed or water-fed parasitoids. Similar results were recorded for *T. pretiosum* Riley (Ashley and Gonzales 1974). Compared to many other parasitoid species, including some species of *Trichogramma*, *T. minutum* does not host feed to any appreciable extent (Corrigan, unpublished). This observation, and the fact that a protein source did not improve their longevity or progeny production, suggest that the females receive sufficient protein for their adult lives from their pre-adult feeding.

Improvements in lifetime offspring production in the carbohydrate treatments are a result of extension of the females' lives in which they produced only a few offspring per day. The differences among treatments for the number of offspring produced in the first 2 days are small in comparison to differences in lifetime reproduction. This suggests that there is little benefit in feeding adults in a mass-rearing program because, in mass culture, a specific batch of parasitoids is generally presented to hosts for no more than 24 h. Even if rearing techniques were changed to accommodate females for longer periods, increases in

productivity of useful parasitoids with respect to field releases (i.e., females) may be limited. In all our experiments, long-lived females produced broods with significantly more male-biased sex ratios than short-lived females and this was especially noticeable beyond 6 days after emergence (Leatemia et al. 1995). This phenomenon has been observed for several species of long-lived parasitoids, including *T. minutum* (Houseweart et al. 1983; Lim 1986; Smith and Hubbes 1986; Bai and Smith 1993). The shift means that actual differences in total numbers of females produced per parasitoid are not as great as the total differences in offspring production. Honey-fed females produce about 99 female offspring per lifetime, whereas unfed females produce 65 female offspring per lifetime. Although that could result in a 50% increase in female offspring per parasitoid, rearing systems would have to be modified to hold parasitizing females for up to 14 days, because this is the period during which female offspring may be produced by the long-lived parasitoids (Leatemia et al. 1995).

The best lifetime offspring production of honey-fed females was recorded at 20 and 25°C, but short-term (2 days) offspring production was maximum at 30°C. This may be of some value in mass production: if feeding is incorporated into the system, it would be relatively easy to increase the temperature in the parasitization arena. The higher short-term offspring production at 30°C was possibly a result of greater activity at this temperature. Optimum lifetime reproduction occurred at 20–25°C, likely because these temperatures represented the best balance between utilization of resources for metabolism and suitable temperatures for egg production and parasitoid activity. Studies comparing parasitization activity at different temperatures have arrived at similar optimum temperature ranges for offspring production (Ram and Sharma 1977; Pintureau et al. 1981; Cabello and Vargas 1988; Wang 1988).

Short-term offspring production was better for honey-fed adults held at 60% and 80% RH than at 20% or 40% RH; thus increasing the relative humidity in the parasitization arenas might provide some improvement in mass production of parasitoids. If both temperature and relative humidity produced additive effects, female production might be enhanced by as much as 25%. It must be pointed out that our data were obtained from females held individually with a surplus of host eggs. In a mass-rearing system, factors such as interference, searching efficiency, and superparasitism could reduce the potential improvements of changing temperatures and humidities on the yields of female offspring.

Based on a laboratory comparison between unfed females of *T. evanescens*, and females provided food for their entire adult lives, Lund (1934) concluded that feeding parasitoids before liberation would increase their effectiveness in the field. Smith et al. (1986) found that females of *T. minutum*, provided with honey for their entire lifespan in field cages, parasitized a significantly higher percentage of spruce budworm egg masses than unfed parasitoids. Results of our study in the laboratory suggest that feeding parasitoids for a short time before a field release would not result in any significant increase in their offspring production compared to unfed parasitoids. Ashley and Gonzales (1974) found that the fecundity of *T. pretiosum*, provided with honey for 1.5 h after emergence, was not significantly different from that of unfed parasitoids. Current release methods are targeted toward the distribution of parasitized host eggs (Hope et al. 1990). Our results suggest that development of mass-release systems for adults would not be justified solely on the ability to feed the adults before release. Providing parasitoids with food in the field throughout their entire lives might increase parasitization, although this may not be practical.

We conclude that although provisioning adult *T. minutum* with honey greatly increased their lifetime offspring production over unfed adults, this improvement is unlikely to increase adult production in a mass-rearing system. The rearing system would have to be modified to incorporate feeding and to hold parasitoids long enough to realize their greater reproductive efforts. Such modifications might be more expensive than the increases in

production would warrant. Potential increases in yields of female progeny through minor adjustment of temperature and humidity would have to be tested in the mass-rearing system to determine if these factors still operated in situations of high-density, scramble competition for hosts. The efficacy of field releases would not be improved by pre-release feeding and it is questionable whether the cost of providing continuously available carbohydrate sources in the field would be justified by the degree of increased parasitism.

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