

Article

Effect of Carbohydrate Nutrition on Egg Load and Population Parameters of Four *Trichogramma* Species

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Abstract: *Trichogramma* parasitoids are the most widely used biocontrol agents and play a crucial role in the biological control of agricultural and forest pests. Many studies have shown that *Trichogramma* parasitoids feeding on carbohydrate rich diet can effectively improve their egg laying capacity and longevity. However, few studies have reported the impact of carbohydrate-rich diet on the biological parameters of different species of *Trichogramma* parasitoids. In this study, we compared the differences between the biological parameters of four *Trichogramma* species (*T. dendrolimi*, *T. chilonis*, *T. leucaniae* and *T. ostriniae*) before and after feeding on carbohydrate-rich diet. The results showed that all the biological parameters of *Trichogramma* species improved after feed on carbohydrate-rich diet. After eclosion, *T. dendrolimi* had the highest egg load (51.89 eggs) followed by *T. chilonis* (26.86 eggs), *T. ostriniae* (24.71 eggs), and *T. leucaniae* (12.44 eggs). *Trichogramma dendrolimi* showed an increased trend in egg load (66.7–86.21 eggs) after feeding on carbohydrate-rich diet, followed by *T. chilonis* (33.12–45.56 eggs), as compared to the other three species. Furthermore, *T. leucaniae* and *T. ostriniae* benefited much less from the ingestion of carbohydrate-rich diet, as only accelerated egg maturation in *T. ostriniae* was observed. Most of the egg loads consisted of matured eggs, so the trend of mature eggs was the same as that of the egg load. We also tested the population parameters of the *Trichogramma* species using the TWOSEX-MSChart. The results showed that the *Trichogramma* species fed with a honey diet had higher fecundities, i.e., *T. dendrolimi* (146.64), *T. chilonis* (173.53), *T. leucaniae* (83.69), and *T. ostriniae* (80.45), than when fed with water, i.e., 78.49, 40.15, 32.45 and 35.47, respectively. *T. dendrolimi* and *T. chilonis* had a higher intrinsic rate of increase r (0.4178 d^{-1} , 0.3933 d^{-1}), finite rate of increase λ (1.5186 d^{-1} , 1.4818 d^{-1}), and net reproductive rate R_0 (130 offspring, 147.4 offspring), than *T. leucaniae* and *T. ostriniae* ($r = 0.3373 \text{ d}^{-1}$, 0.3317 d^{-1} ; $\lambda = 1.4011 \text{ d}^{-1}$, 1.3934 d^{-1} ; $R_0 = 73.2$ offspring, 68.1 offspring) after feeding on a honey diet. We conclude that carbohydrate-rich diet significantly enhanced the biological control efficacy of *Trichogramma*, but the performance differed among different species. The results of this study contribute to improving the efficient application of *Trichogramma* parasitoids in the field.



Citation: Wang, Y.; Iqbal, A.; Mu, M.-Y.; Zang, Z.-Y.; Hou, Y.-Y.; Zang, L.-S. Effect of Carbohydrate Nutrition on Egg Load and Population Parameters of Four *Trichogramma* Species. *Agronomy* **2022**, *12*, 3143. <https://doi.org/10.3390/agronomy12123143>

Academic Editors: Bin Tang, Xiaoling Tan, Yifan Zhai and Michele Ricupero

Received: 5 November 2022

Accepted: 7 December 2022

Published: 10 December 2022

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Keywords: *Trichogramma*; egg load; carbohydrate nutrition; two-sex life table



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1. Introduction

Biological control methods have been utilized worldwide to provide sustainable control of multiple major agricultural pests [1]. The genus *Trichogramma* (Hymenoptera: Trichogrammatidae) is one of the key genera of egg parasitoids broadly used for the biological control of various pests [2,3]. *Trichogramma* have been widely used in more than 50 countries to control Lepidoptera pests in agricultural ecosystems such as those that produce cotton, corn, sugarcane, vegetables, and fruit trees [4–6]. In northeastern China, the release of *Trichogramma* for the control of corn borers increased from an area of 600,000 to 5,500,000 ha during 2005–2015 [2], enabling a decrease in the application of

insecticides, which are known to be harmful to beneficial arthropods [7,8]. In recent years, the technology used for the mass production of *Trichogramma* on an industrial scale has made significant progress in China [9,10]. The mass production of *Trichogramma* mainly relies on mechanized processes, species identification, the use of manually extracted host eggs from *A. pernyi* females, and technology developed for the diapause [11–16]. There are many qualitative evaluation indexes for *Trichogramma* production.

Regardless of whether the parasitoids are in their natural habitat or released under artificial conditions, some individual parasitoids find hosts immediately or soon after being released, while other individuals do not find hosts quickly. Due to the limited resources available, parasitoids require a trade-off between survival and reproduction. In the trade-off hypothesis, there is a negative correlation between survival and reproductive functions [17,18]. Therefore, when the environmental conditions are unfavorable, many parasitoids show the characteristics of the reabsorbing internal egg nutrients to maintain life. Oosorption refers to the phenomenon of reabsorption of mature eggs by the adult itself, which exists in many insects [19,20]. For example, when *Nasonia vitripennis* lack a host, the eggs will be absorbed 2–3 days after maturity [21]. In addition, in *Aphytis melinus*, egg absorption was terminated immediately when they were allowed to feed on the host or even when provided water and honey [22]. In the polyembryonic parasitoid *Copidosoma koehleri*, environmental conditions experienced during development were indeed found to influence resource allocation to egg maturation [23]. Therefore, parasitoids have the ability to autonomously control the production and development of eggs according to the external environmental conditions [24]. However, autonomous regulation of egg development in the ovaries of *Trichogramma* has not been reported. Therefore, the dynamic changes in egg load and the number of mature eggs in *Trichogramma* with time have important reference value for the study of the autonomous regulation of egg development.

Adult parasitoids have two sources of nutrients, one is “capital nutrients”, i.e., nutrients obtained during the growth and development of the host, and second is “income nutrients”, i.e., nutrients obtained during the feeding of the adults [25,26]. Synovigenic parasitoids have relatively low capital nutrition, and the longevity and reproduction of adult females mainly depends on adult feeding. Most egg parasitoids, which have been considered pro-ovigenic, are in fact a moderately synovigenic [27]. Researchers have shown that *Trichogrammatid* are moderately synovigenic [28]. *Trichogramma* wasps have some immature eggs in their ovary when they are recently emerged. [29]. Newly emerged *Trichogramma* adult females feed on other nutrients, which cause the immature eggs to continue to mature, and the number of eggs in the ovaries continues to increase [30–34]. Finally, *Trichogramma* reaches a dynamic equilibrium of survival and reproduction.

Longevity and fecundity are important biological parameters used to directly assess the quality of parasitoids [35], and these parameters are influenced by nutrition [36–38]. Most parasitoids depend on carbohydrates as an energy source for various life activities and physiological processes [39,40]. It is known that the longevity and fecundity of parasitoids are influenced by the composition of sugars, but adults may respond differently to different sugars [41–45]. Carbohydrate rich diets contain monosaccharides, disaccharides, and oligosaccharides, which are provided to fulfill the energy requirements of parasitoids [46,47]. Adults of *Trichogramma* are known to feed on floral nectar, extrafloral nectar [48], and honeydew [49,50]. Fructose, glucose, and sucrose are the most common sugar components in nectars and honeydews [51], and these components can extend the longevity [52–54] and fecundity [55,56] of parasitoids. Many studies have been carried out to evaluate the impact of carbohydrate-rich diet on *Trichogramma* parasitoids longevity and fecundity, however, few studies have documented the impact of carbohydrate-rich diet on the population parameters of the *Trichogramma* species used in the TWSEX-MSChart.

The life table is a type of research tool that is frequently used in many studies involving population and community ecology [57,58]. Accurate life table analyses are important for correctly evaluating the overall fitness of populations. Traditional female age-specific life tables ignore the male individuals in a population that is a defining characteristic of insects.

Their application to data analysis involving these groups inevitably results in miscalculations and limits the practical application of these life tables, but TWOSEX-MSChart can correct such errors [59]. Therefore, we tested the fecundity, longevity, and other parameters of *Trichogramma* using the TWOSEX-MSChart. However, a deeper understanding of how parasitoids cope with the trade-off between survival and reproduction in the wild is more conducive to the efficient and low-cost application of parasitoids. Therefore, we evaluated the impacts of fructose (monosaccharide) and honey (mixed-sugar) diets on the population parameters of different *Trichogramma* species in this study.

Previously, most studies focused on the effects of carbohydrate-rich diet on the longevity and fecundity of *Trichogramma*, while few studies have focused on the impacts of a carbohydrate diet on the biological parameters among different *Trichogramma* species. In this study, we conducted experiments with four *Trichogramma* species (*T. dendrolimi*, *T. chilonis*, *T. ostriniae*, and *T. leucaniae*), which usually occur in different crop fields. To evaluate the impact of carbohydrate-rich diet on the biological parameters of *Trichogramma* species, we investigated the dynamic changes in the egg load, number of mature eggs and population parameters. This study contributes to the efficient application of *Trichogramma* parasitoids in the field.

2. Materials and Methods

2.1. Parasitoids

Trichogramma leucaniae were collected in soybean fields from parasitized eggs of soybean pod borers *Leguminivora glycinivorella* Matsumura (Lepidoptera: Tortricidae) in Heilongjiang Province. *Trichogramma ostriniae* and *T. dendrolimi* were collected from parasitized eggs of *Ostrinia nubilalis* in Changchun, Jilin Province. *Trichogramma chilonis* was collected from Heihe, Heilongjiang Province. Identification of the four species was performed by analyzing the morphology of male genital capsules [60]. The *Trichogramma* species were reared for up to 10 generations on *C. cephalonica* eggs under laboratory conditions. The laboratory conditions were 25 ± 1 °C temperature, $70 \pm 5\%$ relative humidity, and an L14:D10 photoperiod [10]. Newly emerged female wasps were collected within only a 30 min period for culturing in the morning for there to be as much synchronization as possible between them.

2.2. Hosts

To obtain host eggs of the rice moth *Corcyra cephalonica* for breeding the *Trichogramma* species, larvae of rice moth were placed in plastic containers in which they were fed with a mixture of cornmeal and wheat bran. Rice moth adults were collected after emergence and transferred to aluminum mesh cages to lay eggs. Rice moth eggs were collected in trays. Fresh rice moth eggs collected daily were exposed to 40 W UV light for 45 min to kill the embryos, and the eggs were used to breed *Trichogramma* parasitoids [61]. Rice moth eggs were glued onto strip-shaped egg cards (2 cm × 1 cm) used for all the experiments.

2.3. Egg Load and Mature Eggs

Four treatments were assigned in this experiment. In two treatments, all four *Trichogramma* species were fed with carbohydrate-rich diets, i.e., with honey water solution (20%) and fructose water solution (20%), separately. In another two treatments, one treatment was assigned where all four *Trichogramma* species were fed only with water and in the other, the *Trichogramma* species were deprived of any kind of food. The parasitoids were kept in an incubator set to 25 ± 1 °C, $70 \pm 5\%$ RH, and a L14:D10 photoperiod to allow them to develop. At 0, 4, 8, 12, 16, 20, 24, 48, and 72 h, the ovaries of *Trichogramma* females were dissected. The female's adult ovipositor was pulled out using needles, until both the ovipositor and the ovaries were detached from the abdomen. The ovaries were placed on a microscope slide with a ringer solution (NaCl 6 g/L; $C_3H_5NaO_3$ 3.1 g/L; KCl 0.3 g/L; $CaCl_2 \cdot 2H_2O$ 0.2 g/L) and were examined under a stereoscope. The ovaries were pressed with a needle until the eggs were expelled, and fully matured eggs were counted

for each of the parasitoids [62,63]. Eggs with a full shape and full yolk were regarded as mature eggs, while eggs without a full shape and insufficient yolk filling were regarded as immature eggs [64,65]. Since the longevity of *Trichogramma* wasps was less than 48 h without feeding with carbohydrate-rich diet, there were no 48 h and 72 h observations in the two treatments, i.e., those fed with only water and deprivation. A total of 30 *Trichogramma* female adults of each species were dissected in each treatment and for each time period, and the overall experiment was repeated 3 times.

2.4. Population Parameters

Our preliminary observations found that honey and fructose as food sources were equally effective. In this experiment, therefore, we selected honey as the food source, and compared the life table parameters between the honey-solution-(20%)-fed wasps and water-fed wasps. This experiment was conducted under the following environmental conditions: 25 ± 1 °C, $70\% \pm 5\%$ RH, and 14 L:10 D photoperiod, where the *Trichogramma* species used were reared from *C. cephalonica* host eggs. In order to obtain the age-specific fecundity of *Trichogramma* on *C. cephalonica* eggs, a pair of newly emerged (<4 h) female and male wasps from each species were first mated in a glass tube (7 × 1 cm, length × diameter) and then provided with 300 *C. cephalonica* eggs (embryos killed by using UV lamp for 40 min) in the tube. The *C. cephalonica* eggs were glued on a strip egg card (2 × 1 cm, length × width). New *C. cephalonica* eggs and the honey water were replaced daily until the death of the female wasp. The exposed egg card from the previous day was transferred to another glass tube, and the population parameters of each wasp were recorded daily. There were 30 wasps in each test, and the experiment was repeated three times.

The age-specific fecundity and cumulative fecundity were the average number of successfully parasitized eggs by all surviving individuals at all age-specific parameters of the population. The fecundity of the population was represented by the average number of successfully parasitized eggs by all individuals. The net reproductive rate (R_0) was the average number of emerged adult offspring for a parasitoid during her lifetime; the intrinsic rate of increase (r) was the growth rate of the population when it reached a stable age-stage distribution; the finite rate of increase (λ) is the average daily growth rate of the population when it reaches the stable age-stage distribution, and the mean generation time (T) was the time required to increase R_0 . The above parameters were calculated according to the life table.

2.5. Data Analysis

The data were subjected to a normality test using the Shapiro–Wilk test prior to ANOVA. The number of eggs loaded and the number of mature eggs in the *Trichogramma* species in the different tests were analyzed using one-way analysis of variance (ANOVA), where the means were separated using Tukey’s honestly significant difference (HSD) test at $p < 0.05$. All the statistical analyses were performed using SPSS 20.0 (SPSS Inc., Chicago, IL, USA).

The data of the population parameters were analyzed according to the two-sex life table method [66–69]. For the estimation of variances and standard errors of all the parameters, the bootstrap technique [70], embedded in TWOSEX-MSChart was used with $B = 100,000$ re-samplings. The significant differences among treatments were assessed using the paired bootstrap test ($p \leq 0.05$) embedded in TWOSEX-MSChart [71,72].

3. Result

3.1. Egg Load

There was no significant difference in the number of eggs loaded by *Trichogramma* species when fed with the honey or fructose solution, when fed with water, or deprived of food. After eclosion, *T. dendrolimi* had the highest number (51.89) of eggs loaded, followed by the other three species, i.e., *T. chilonis* had 26.86, *T. ostrinae* had 24.71, and *T. leucaniae* had 12.44 eggs loaded, respectively (Figure 1). The egg loads in all the *Trichogramma* species increased rapidly from 0 to 4 h. *Trichogramma dendrolimi* showed the highest increase trend

in egg load after being fed with the honey and fructose solution in comparison to the other three species. The *Trichogramma dendrolimi* and *T. chilonis* egg loads showed the same trend with time, which increased at first and then decreased (Figure 1).

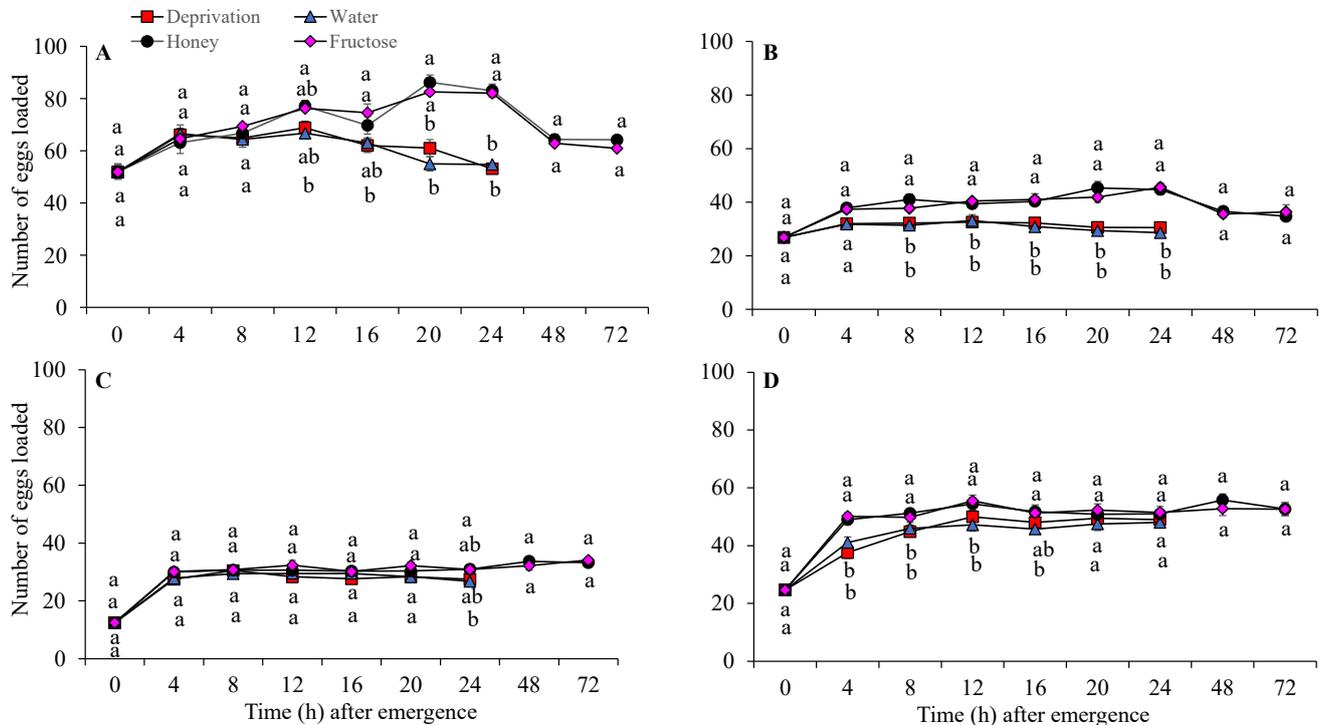


Figure 1. Impact of carbohydrate-rich diet on the egg load of four *Trichogramma* species with time. *T. dendrolimi* (A), *T. chilonis* (B), *T. leucaniae* (C), and *T. ostriniaie* (D). The number of egg loads was given as mean \pm SE. Different lowercase letters in each figure indicate significant differences among different treatments (Tukey's HSD test, $p < 0.05$).

Trichogramma dendrolimi increased their number of eggs up to 86.21 (20 h) and 82.53 (20 h), respectively, after being fed with the honey and fructose solution, whereas, for the water-fed and deprived wasps, the number of eggs increased up to 66.7 (12 h) and 68.81 (12 h), respectively (Figure 1A). The carbohydrate-rich diet significantly increased the egg load of *T. dendrolimi* in the period of 12 to 24 h (12 h: $F_{3,84} = 3.797$, $p = 0.0176$; 16 h: $F_{3,81} = 6.722$, $p = 0.0011$; 20 h: $F_{3,91} = 19.351$, $p < 0.0001$; 24 h: $F_{3,90} = 42.056$, $p < 0.0001$). *Trichogramma chilonis* increased their number of eggs from 26.86 (0 h) to 45.33 (20 h) and 45.56 (24 h), respectively, after being fed with honey and fructose, whereas for the water-fed and deprived wasps, the increase in eggs was from 26.86 (0 h) to 32.5 (12 h) and 33.13 (12 h), respectively (Figure 1B). The carbohydrate-rich diet significantly increased the egg load of *T. chilonis* in the period of 12 to 24 h (8 h: $F_{3,84} = 11.381$, $p < 0.0001$; 12 h: $F_{3,84} = 4.947$, $p = 0.0068$; 16 h: $F_{3,81} = 8.691$, $p = 0.0003$; 20 h: $F_{3,91} = 23.607$, $p < 0.0001$; 24 h: $F_{3,90} = 35.337$, $p < 0.0001$).

For *T. ostriniaie* and *T. leucaniae*, the egg loads were relatively stable 4 h after emergence. The egg loads of *T. ostriniaie* and *T. leucaniae* did not increase significantly after feeding on the carbohydrate-rich diet. The carbohydrate-rich diet had only a slight effect on the egg load of *T. leucaniae*, but there was no significant difference (Figure 1C). However, a significant increase in the egg development rate in *T. ostriniaie* species was observed (Figure 1D) (4 h: $F_{3,94} = 10.797$, $p < 0.0001$; 8 h: $F_{3,90} = 4.25$, $p = 0.0088$; 12 h: $F_{3,90} = 7.765$, $p = 0.0003$).

3.2. Mature Eggs

Generally, the number of mature eggs and the number of eggs loaded by the *Trichogramma* species had the same trend with time. At eclosion, the percentage of mature

eggs in the egg load of *T. dendrolimi* was 74.29%; in *T. chilonis*, it was 59.11%; in *T. leucaniae*, it was 70.54%; and in *T. ostrinia*, it was 55.54%, respectively. At 4 h after emergence, the percentage of mature eggs in the egg load of the four *Trichogramma* species was above 80%, which showed that there was no significant difference in the trends of number of the mature eggs and egg load among the species.

In addition, a significant increase in the mature eggs of *T. dendrolimi* was observed in the period of 16 to 24 h after being fed with the carbohydrate-rich diet (16 h: $F_{3,81} = 16.097$, $p < 0.0001$; 20 h: $F_{3,91} = 10.507$, $p = 0.0001$; 24 h: $F_{3,90} = 8.346$, $p = 0.0001$) (Figure 2A). In *T. chilonis*, mature eggs were significantly increased during the 20–24 h period (20 h: $F_{3,94} = 6.226$, $p = 0.0017$; 24 h: $F_{3,90} = 19.665$, $p < 0.0001$) (Figure 2B). In *T. leucaniae*, mature eggs were not significantly increased from 4 to 24 h (Figure 2C). In *T. ostrinia*, mature eggs were significantly increased during the 4–8 h period (4 h: $F_{3,94} = 12.233$, $p < 0.0001$; 8 h: $F_{3,90} = 8.323$, $p = 0.0001$) (Figure 2D).

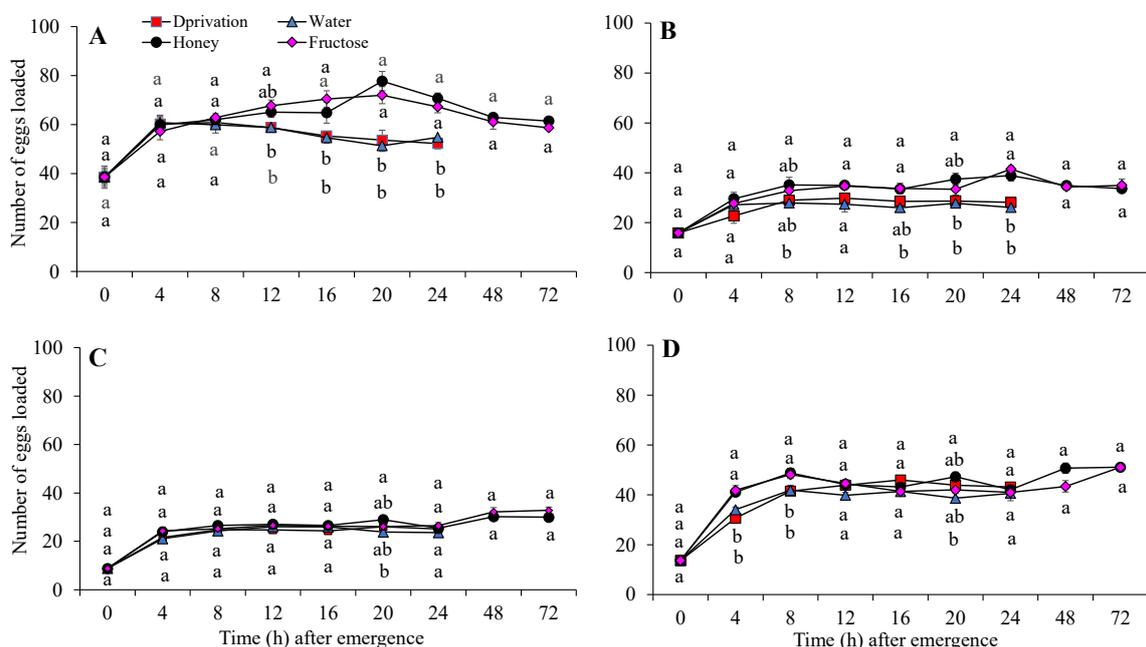


Figure 2. Impact of carbohydrate-rich diet on the egg maturity of four *Trichogramma* species with time. *T. dendrolimi* (A), *T. chilonis* (B), *T. leucaniae* (C), and *T. ostrinia* (D). Number of mature eggs was given as mean \pm SE. Different lowercase letters in the figure indicate significant differences among different treatments (Tukey's HSD test, $p < 0.05$).

3.3. Population Parameters

The population parameters of the *Trichogramma*, fed with honey were significantly better than those fed with water (Table 1). The female adult longevity of *T. ostrinia* was 2.05 days higher than that of the other species fed with water. The female adult longevity of *T. ostrinia* and *T. chilonis* was 15.48 and 15.33, respectively. This was days higher than that of the other species when fed with honey. After being fed with honey, the fecundity of *T. dendrolimi* increased from 78.49 to 146.64, and for *T. chilonis*, it increased from 40.15 to 173.53, where the fecundity of *T. chilonis* exceeded that of *T. dendrolimi* and remained the highest. In terms of oviposition days, the longest oviposition duration (13.88 days) was recorded for *T. chilonis*, and the shortest (9.39 days) was recorded for *T. dendrolimi* when fed with honey. On the other hand, the oviposition days of *T. chilonis* and *T. dendrolimi* were only 1.33 and 1.61, respectively, when fed with water.

Table 1. Parameters of four *Trichogramma* species fed with honey solution and water parasitizing on *Corcyra cephalonica* eggs.

Parameter	<i>T. dendrolimi</i>		<i>T. chilonis</i>		<i>T. leucaniae</i>		<i>T. ostrinae</i>	
	Honey	Water	Honey	Water	Honey	Water	Honey	Water
Female adult longevity (days)	10.18 ± 0.23 ^c	1.61 ± 0.08 ^e	15.33 ± 0.23 ^a	1.33 ± 0.34 ^f	13.05 ± 0.25 ^b	1.79 ± 0.07 ^e	15.48 ± 0.30 ^a	2.05 ± 0.08 ^d
Fecundity (<i>F</i>)	146.64 ± 1.89 ^b	78.49 ± 1.60 ^c	173.53 ± 5.26 ^a	40.15 ± 0.39 ^d	83.69 ± 3.43 ^c	32.45 ± 1.33 ^f	80.45 ± 3.32 ^c	35.47 ± 0.73 ^e
Oviposition days	9.39 ± 0.22 ^c	1.61 ± 0.08 ^e	13.88 ± 0.21 ^a	1.33 ± 0.34 ^f	10.18 ± 0.37 ^c	1.79 ± 0.07 ^e	11.33 ± 0.28 ^b	2.05 ± 0.08 ^d
Net reproduction rate (<i>R</i> ₀) (offspring)	130.0 ± 4.8 ^b	68.9 ± 2.7 ^c	147.4 ± 7.3 ^a	33.3 ± 1.5 ^d	73.2 ± 4.0 ^c	28.5 ± 1.1 ^e	68.1 ± 3.6 ^c	29.4 ± 1.4 ^{de}
Intrinsic rate of increase <i>r</i> (day ⁻¹)	0.4178 ± 0.0048 ^a	0.3895 ± 0.0049 ^b	0.3933 ± 0.0048 ^b	0.3301 ± 0.0048 ^c	0.3373 ± 0.0049 ^c	0.2918 ± 0.0045 ^d	0.3317 ± 0.0053 ^c	0.2940 ± 0.0047 ^d
Finite rate of increase (<i>λ</i>) (day ⁻¹)	1.5186 ± 0.0133 ^a	1.4761 ± 0.0070 ^b	1.4818 ± 0.0070 ^b	1.3911 ± 0.0067 ^c	1.4011 ± 0.0068 ^c	1.3388 ± 0.0060 ^d	1.3934 ± 0.0073 ^c	1.3417 ± 0.0063 ^d
Mean generation time (<i>T</i>) (days)	11.65 ± 0.10 ^b	10.87 ± 0.09 ^c	12.69 ± 0.14 ^a	10.62 ± 0.07 ^d	12.73 ± 0.12 ^a	11.46 ± 0.11 ^b	12.72 ± 0.13 ^a	11.49 ± 0.10 ^b

Values are mean ± SE, and different letters within the same row indicate significant differences between treatments (bootstrap test, $B = 100,000$, $p < 0.05$).

The net reproduction rate (R_0) of *T. chilonis* was significantly higher than that of the other species. After feeding on honey, the R_0 of *T. dendrolimi* increased from 68.9 to 130.0 and for *T. chilonis*, it increased from 33.3 to 147.4. For *T. leucaniae*, it only increased from 28.5 to 73.2, and for *T. ostrinae*, it only increased from 29.35 to 68.08. The intrinsic rate of increase (r) and the finite rate of increase (λ) in *T. dendrolimi* were the highest, while the mean generation time (T) was the shortest. When fed with honey, the r of *T. dendrolimi* increased from 0.3895 to 0.4178, the λ increased from 1.4761 to 1.5186, and the T increased from 10.87 to 11.65.

3.4. Age-Specific Fecundity and Cumulative Fecundity

The age-specific fecundity of *Trichogramma* parasitizing *C. cephalonica* eggs is presented in Figure 3. As it is known that only adult female *Trichogramma* are fecund, the curves for the age-specific fecundity and cumulative fecundity were all zero before the adult stage. When the water was provided to the wasps, the peaks of the age-specific fecundity of *T. dendrolimi*, *T. chilonis*, and *T. leucaniae* reared on the *C. cephalonica* eggs were 25.87, 15.51, and 9.20, respectively, per parasitoid at the age of 11 days, while for the *T. ostrinae* species, it was 9.66 at the age of 12 days (Figure 3A). In the four parasitoid species, the age-specific fecundity of *T. dendrolimi* was the highest whether fed with water (25.87) or honey (35.68) at the age of 11 days (Figure 3B). It is noteworthy that for the age-specific fecundity of *T. chilonis*, there were two peaks, i.e., at day 11 (28.42) and day 16 (13.73) (Figure 3B).

The cumulative fecundity is presented in Figure 4. The cumulative fecundity of the parasitoids fed with honey solution was significantly higher than that of the parasitoids fed with water. For all four species, when they were fed with water, the cumulative fecundity did not increase after 16 days (Figure 4A), but when they were fed with the honey solution, the cumulative fecundity did not increase after 29 days (Figure 4B). In the four parasitoid species, the cumulative fecundity of *T. dendrolimi* species was the highest (68.89, after 15 days) when fed with water, while it was the highest (147.39, after 27 days) for *T. chilonis* after being fed with the honey solution. *T. dendrolimi* and *T. chilonis* had higher fecundities than *T. leucaniae* and *T. ostrinae*, regardless of whether they were fed with water or honey.

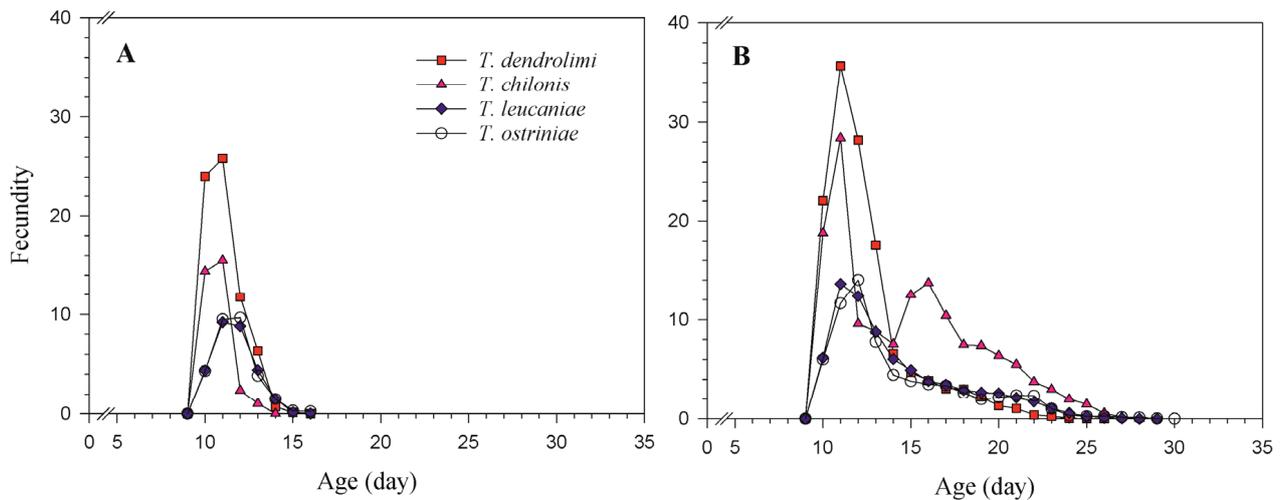


Figure 3. Age-specific net reproductive rate of the population of four *Trichogramma* species parasitizing *C. cephalonica* eggs. Fed with water (A) and fed with honey (B).

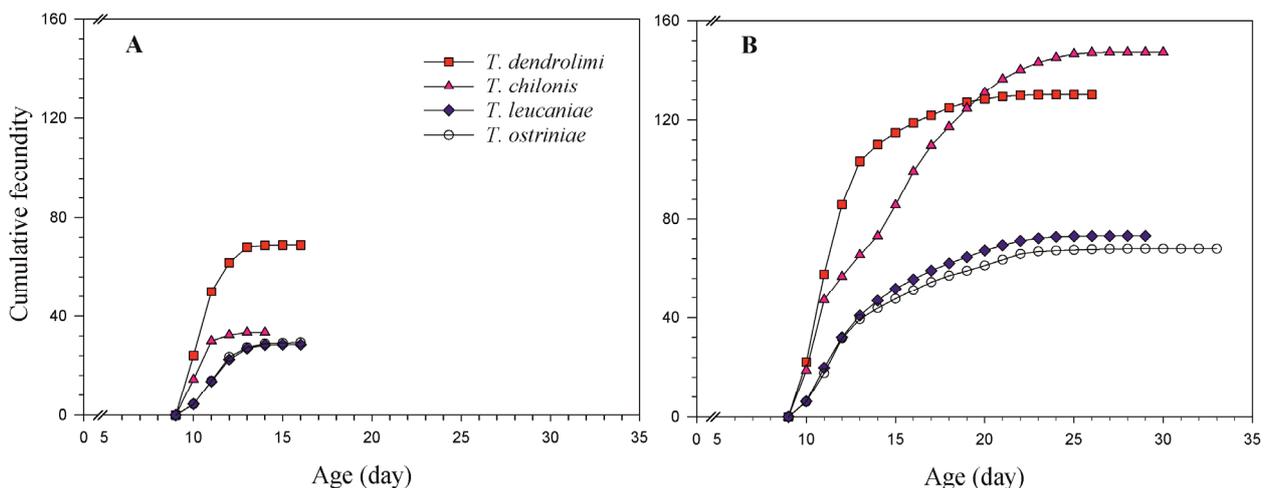


Figure 4. Cumulative fecundity of four *Trichogramma* species parasitizing *C. cephalonica* eggs. Fed with water (A) and fed with honey (B).

4. Discussion

In this study, we compared the demographic parameters and egg loads of four *Trichogramma* species after being fed a carbohydrate-rich diet. The results showed that carbohydrate nutrients had a significant impact on the biological parameters of adult *Trichogramma*, however, different *Trichogramma* species responded differently. The intake of carbohydrate nutrients can enhance the biological control potential of *Trichogramma* to a large extent.

To compare the impact on the egg load of the four *Trichogramma* species in different treatments, we found that the intake of honey and fructose effectively improved the egg load of the *Trichogramma* species. Although some studies showed that different sugars had different effects on parasitoids [53], our experiments proved that fructose and honey had the same effects on the four *Trichogramma* species. Many researchers have evaluated the potential fecundity of parasitoid wasps according to the number of eggs loaded [73–76]. In our study, the egg load of *T. dendrolimi* was higher than that of *T. chilonis* when they were fed with honey, but the cumulative fecundity of *T. chilonis* was higher than that of *T. dendrolimi*. Mills and Kuhlmann (2000) showed the same results for *T. pretiosum* [77]. These results indicated that the number of eggs loaded cannot replace the number of eggs laid as an evaluation index of fecundity, but only as a reference value for evaluation.

Although the number of eggs loaded cannot directly evaluate fecundity, it can well reflect other life activity parameters. Previous studies showed that egg load had significant effects on insect reproductive behavior. Females with a high egg load typically put more effort into finding a host and are less particular about host quality than females with a low egg load [78–83]. Our study also confirmed these results, where *T. dendrolimi* had the highest egg load and a broader host range, while *T. leucaniae* and *T. ostrinia* had a lower egg load and a narrower host range. The number of eggs loaded by *T. dendrolimi* and *T. chilonis* increased significantly after feeding on carbohydrates, while the number of eggs loaded by *T. leucaniae* and *T. ostrinia* did not change significantly, which may be related to their unique ovarian structure. Many researchers have attempted to characterize the effects of an insect's internal structure on their oviposition behavior and egg load [84–86]. Research regarding dynamic ovarian development has come into focus [87–89].

The dynamic change in egg load can reflect the trade-off between the survival and reproduction of parasitoids in different living environments. In nature, parasitoids face a trade-off between survival and reproduction because of their limited resources. In our study, when the *Trichogramma* species were fed with honey and fructose, their egg loads increased, which indicated that the species directly chose to reproduce when their survival was not threatened. In the life history of insects, there exists a trade-off between life activities and functions, which is usually manifested as a negative correlation between survival and reproduction [18]. However, this hypothesis has rarely been tested in Hymenoptera parasitoids [90,91]. In this study, the dynamic changes in the egg loads of the *Trichogramma* species with time were different in two states, i.e., survival without stress and survival under stress. Most of the egg loads consisted of mature eggs, so the number of eggs loaded could be expressed as the investment of *Trichogramma* in early life reproduction to some extent [92]. *Trichogramma dendrolimi* had the highest initial egg load, indicating that they prefer early life reproduction and invest more resources in reproduction at an early stage, while *T. chilonis* prefer late reproduction and invests more resources in survival at an early stage. The changes in the number of mature eggs and egg load indicated that oogenesis and oosorption simultaneously occur in *Trichogramma*. Some researchers also found that many parasitic wasps, such as the *Encarsia formosa* Gahan [93] and the *Bombyx mandarina* Leech [94], can promote oogenesis and slow egg reabsorption after feeding on sugar. Similarly, when *Trichogramma* have enough energy, their survival is not threatened, and they may distribute more nutrients to their offspring. Therefore, *Trichogramma* fed with carbohydrates are beneficial for the reproduction of field populations. Our study lays the foundation for further understanding the survival-reproduction trade-off mechanism in *Trichogramma*.

The two-sex life table analysis allows a thorough understanding of the demography and parasitic effectiveness of *Trichogramma* and comparisons between some important life-history traits and key demographic parameters of the parasitoids fed with carbohydrates and water. In this study, fructose and honey had the same effect on the egg load of *Trichogramma*; only the honey solution was used in the diet to evaluate its impact on the fecundity and other parameters of *Trichogramma* in the later stage. Most of these key demographic parameters, such as female adult longevity, ovipositional days, fecundity, and cumulative fecundity rate, were higher when the *Trichogramma* species were fed with the honey solution as compared to when they were fed with water (Figure 3). In all four *Trichogramma* species fed with water, their fecundity declined 2 days after emerging, and the cumulative fecundity stabilized 3 days after emerging because most of the wasps were already dead. When they were fed the honey solution, however, the cumulative fecundity stabilized 15 days after emerging. These results indicated that the parasitoids had higher per capita reproductive potential when they were fed honey in comparison to water. Previously, many studies reported that parasitoids rely mainly on carbohydrates to meet their nutritional requirements, and carbohydrates have a large impact on their lifespan and reproduction [95–98]. Some studies similarly concluded that parasitoids may search for and feed on nectar and honeydew, which can have a beneficial impact on the population

level parasitism of the target pests [99]. Here, we further confirmed that the feeding of *Trichogramma* parasitoids on honey carbohydrate is beneficial for the reproduction of the field population. By comparing the four species, the life table parameters of *T. dendrolimi* and *T. chilonis* were found to be better than those of *T. leucaniae* and *T. ostrinia*. However, *T. dendrolimi* had the shortest lifespan, possibly due to its preference for early life reproduction, allocating more resources to reproduction, thereby leading to a shorter lifespan.

The interesting result was that the cumulative fecundity of *T. chilonis* was lower than that of *T. dendrolimi* when their wasps were fed with water, but the cumulative fecundity of *T. chilonis* was higher than that of *T. dendrolimi* when their wasps were fed with the honey solution. *Trichogramma chilonis* had two fecundity peaks after being fed with the honey solution, which was the reason for its cumulative fecundity exceeding that of *T. dendrolimi* in the late stage. These results suggested that the two parasitoid species had different trade-offs between survival and reproduction, i.e., *T. dendrolimi* prefers early life reproduction, while *T. chilonis* prefers late reproduction. Similarly, the fecundity of *T. ostrinia* reached the highest at 3 days after emergence, while that of the other three species it reached the highest at 2 days. In the four *Trichogramma* species, *T. dendrolimi* had the highest egg load when they first emerged, but the shortest longevity. Thus, the hypothesis that synovigenic species are longer-lived than pro-ovigenic ones has been confirmed, as well as the hypothesis that the ovigeny index and life span are negatively correlated across parasitoid taxa, suggesting a cost to the life span when concentrating reproductive efforts early in adult life [27,89]. These results are supported by the results obtained from fecundities and egg loads in our study.

5. Conclusions

In this study, the effects of carbohydrate nutrition on various biological parameters of four *Trichogramma* species were compared. After eclosion and being fed a carbohydrate-rich diet, the egg loads of *T. dendrolimi* and *T. chilonis* increased significantly, while the carbohydrate-rich diet had no impact on the egg loads of *T. ostrinia* and *T. leucaniae*. In the comparison between the two-sex life table parameters of the four *Trichogramma* species fed carbohydrate-rich diet, *T. dendrolimi* and *T. chilonis* performed the best, followed by *T. ostrinia* and *T. leucaniae*. Carbohydrates were found to accelerate the egg development of *Trichogramma*, effectively increase their egg load, extend the biological control time, and improve their fecundity and longevity, but with different effects on different *Trichogramma* species. Based on our results, therefore, we recommend planting flowering plants in the field so as to improve the biocontrol effect of *Trichogramma* and to provide good conditions for colonization by wasps in the field. Our study provides a theoretical basis for the efficient use different species of *Trichogramma* in the field.

Author Contributions: Conceptualization, L.-S.Z. and Y.-Y.H.; methodology, Y.W., Y.-Y.H. and L.-S.Z.; validation, L.-S.Z.; formal analysis, L.-S.Z.; investigation, Y.W. and Z.-Y.Z.; resources, L.-S.Z.; data curation, Y.W., Z.-Y.Z. and L.-S.Z.; writing—original draft preparation, Y.W. and A.I.; writing—review and editing, L.-S.Z.; visualization, L.-S.Z. and Y.-Y.H.; supervision, M.-Y.M., L.-S.Z. and Y.-Y.H.; project administration, L.-S.Z.; funding acquisition, M.-Y.M. and L.-S.Z. All authors have read and agreed to the published version of the manuscript.

Funding: This study was partially funded by the National Natural Science Foundation of China (32172469), and Natural Science Research Program of Guizhou University (202202).

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest.

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