

Effects of Five Naturally Occurring Sugars on the Longevity, Oogenesis, and Nutrient Accumulation Pattern in Adult Females of the Synovigenic Parasitoid *Neochrysocharis formosa* (Hymenoptera: Eulophidae)

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Abstract

Neochrysocharis formosa (Westwood) (Hymenoptera: Eulophidae), one of the dominant natural enemies of agromyzid leafminers, is a synovigenic parasitoid. We compared the longevity, oogenesis, and nutrient levels of female wasps provided with 10% solutions of five naturally occurring sugars. All five sugars significantly increased the longevity of female wasps, which was 6.5–9.3-fold higher than that of parasitoids provided with water only. We found no significant difference in longevity of female wasps fed on glucose versus fructose or trehalose versus melezitose, but longevity of wasps fed on glucose or fructose was significantly longer than those fed on trehalose or melezitose. Also, we examined the oosorption capability of wasps fed on the five sugars. Some mature eggs were present in the ovaries of newly emerged females, but these were fully reabsorbed within 72 h when wasps were starved. Once wasps were fed with any of the sugars, the number of mature eggs increased at first and then decreased due to oosorption. The longevity and oogenesis dynamics of female wasps fed on five sugars were related with their function of hydrolysis and digestion. As female wasps have no lipogenesis capability, by acquiring exogenous sugars for oogenesis, they can either maintain or exceed the original level of capital nutrients held on adult emergence because none of the wasps' glycogen need be metabolized to burn as sugar.

Introduction

The effectiveness of parasitoids as natural enemies in agroecosystems depends on certain key traits such as fecundity and longevity. Nutrient sources allocated to survival and reproduction can be mobilized from capital reserves acquired during larval feeding, or from resources acquired through adult feeding; the former were called as capital nutrient; the latter were named as income nutrient based on the dichotomy between capital and income breeders (Casas *et al* 2005, Jervis *et al* 2008, Visser & Ellers 2012); therefore, the ways of

nutrients acquired by female wasps influence their longevity and fecundity and then the biocontrol efficacy (Jervis & Ferns 2004, 2011, Casas *et al* 2005).

Parasitoid wasps are highly diverse with respect to a wide array of life-history traits (Jervis & Ferns 2011). Flanders (1950) distinguished proovigenic versus synovigenic parasitoids, based on the number of mature oocytes in the ovaries of female adults at emergence. At emergence, oocytes in the ovaries of proovigenic parasitoids are completely mature, while few or even no oocytes are mature in the ovaries of synovigenic parasitoids. Therefore, the adult females of

synovigenic parasitoids must obtain nutrients for oogenesis and egg maturation through feeding. The degree of synovigeny is given as an ovigeny index (OI) (Jervis *et al* 2001), which is the ratio of the mean egg complement at adult emergence to the mean maximum lifetime egg complement, where $OI=1$ means strictly proovigeny and $OI=0$ means purely synovigeny. In order to body maintenance or offspring reproduction, synovigenic parasitoids usually utilize host food and/or non-host food.

Many studies have confirmed that the nectar, pollen, and insect honeydew can prolong the longevity of female wasps (Lee *et al* 2004, Chen & Fadamiro 2006) and that the sugars from these foods play a pivotal role in this process as energy substances (Baker & Baker 1983, Bugg *et al* 1989, Jervis *et al* 1993, Wäckers *et al* 1996, Wäckers 2001, Chen & Fadamiro 2006, Luo *et al* 2010). Furthermore, wasps with increased longevity have an increase in opportunities to encounter hosts (Idris & Grafius 1995, Giron *et al* 2002, 2004). However, the sugar composition (sugar species and content/quantity) of naturally occurring sugar sources (such as nectar, honeydew, etc.) in the field are quite different (van Handel *et al* 1972, Baker & Baker 1983, Wäckers 2001, Tompkins *et al* 2010). Although the different components of these sugars could affect longevity and fecundity of parasitoids to different extent (Chen & Fadamiro 2006, Luo *et al* 2010, Harvey *et al* 2012), few studies were showed to examine the integrity effects of different sugar components on longevity, reproduction/oogenesis, and physiological functions of parasitoids, especially not considering the difference of those life-history traits of synovigenic parasitoids. Besides, the reproduction of synovigenic parasitoids is often restricted by their limited mature oocytes, resulting in a need for additional nutrients, whose acquisition reduces time available to search hosts (Shea *et al* 1996, van Alphen & Jervis 1996, Heimpel & Rosenheim 1998, Rosenheim *et al* 2000). To maximize the biological control potential of synovigenic parasitoids, agricultural practices should be selected that prolong parasitoid longevity, and promote oogenesis and egg maturation (Heimpel & Collier 1996).

Neochrysocharis formosa (Westwood) (Hymenoptera: Eulophidae), as one of the dominant parasitoids of agromyzid leaf miners, has widely distributed in over 30 countries. It has wide temperature adaptability and strong heat tolerance, enhancing its biological control potential (Chien *et al* 2005, Saleh *et al* 2010, Wang *et al* 2012a). As a typical synovigenic parasitoid, *N. formosa* can feed on both host larvae and non-host foods such as nectar, honeydew, etc. (Chien & Ku 2001, Moon *et al* 2004, Song *et al* 2004). While honey can significantly increase the longevity and fecundity of female wasps (Song *et al* 2004, 2005), the effects of different sugars on the longevity and oogenesis have not been thoroughly evaluated. In this study, we selected the common sugars in nature, compared their effects on *N. formosa* female wasps'

longevity and oogenesis, and investigated their nutrient accumulation pattern. We hypothesize that the longevity and oogenesis dynamics of female wasps fed on five sugars were related with their function of hydrolysis and digestion. It is hoped that the results will improve the biocontrol practice in artificial rearing and conservation of field populations of this important parasitoid.

Material and Methods

Insect cultures

Neochrysocharis formosa adults that emerged from *Liriomyza huidobrensis* (Blanchard) leafmines from a celery field in Gongxian, Yunnan, China, in April 2012, and their progeny were then cultured in second or third instars of *Liriomyza sativae* Blanchard. *Liriomyza sativae* adults were collected from a bean field at the Langfang Experimental Station of the Institute of Plant Protection, Chinese Academy of Agricultural Sciences. Both parasitoids and hosts were reared in a greenhouse on dwarf oil bean, *Phaseolus vulgaris*, at 25–30°C, 70–80% RH, and natural light.

Effects of five sugars on the longevity of N. formosa

Based on the structures and physiological functions of different sugars (Leatemia *et al* 1995, Morales-Ramos *et al* 1996, McDougall & Mills 1997, Wäckers 2001), we selected five common sugars found in naturally occurring in nectar or honeydew (the monosaccharides glucose and fructose; the disaccharides sucrose and trehalose; and the trisaccharide melezitose) for the test. The five sugars are all in analytical purity and the concentration of all sugar solutions was 10% (w/v) as it could be the most common content in floral nectar (Wäckers 2001).

Healthy female wasps at about 10:00AM every day were collected after emergence (less than half an hour old), and individual wasps were placed in tubes (L×dia.=20×2.5 cm) and provided with either sugar solution or water (control) soaked into absorbent cotton. Each tube was covered with 100-mesh gauze and held at $27\pm 0.5^\circ\text{C}$, 70–80% RH, and a 16:8 h L/D photoperiod. Survival was recorded at 10:00AM every day. The sugar diets were changed daily to maintain a constant concentration. Twenty female wasps were tested for each treatment.

Effect of sugars on oogenesis

At 10:00 each day, ten female wasps in each treatment were randomly selected and then rapidly killed by freezing under -20°C refrigeration. Each female's ovary was dissected under a stereoscopic microscope (LX73, Olympus, Tokyo, Japan),

and the number of oocytes was counted. Oocytes were categorized into three ranks reflecting their degree of development (referred to Wang et al 2012b and Liu et al 2014): In rank I eggs, the area of yolk deposition was less than half of the whole volume of egg chamber; in rank II eggs, yolk filled more than half but not all of the egg chamber; rank III eggs (mature eggs) were those in which the chamber was completely full of yolk. *Neochrysocharis formosa* female wasps will not oviposit in the absence of a host (Liu et al 2014).

Effects of five sugars on nutrient content of female wasps

Temporal patterns of accumulation and utilization of energy resources were followed in *N. formosa* females fed on different types of sugars according to the above design section (“Effects of five sugars on the longevity of *N. formosa*”). Daily changes in the amount of fructose, total sugars, glycogen, and total lipids were quantified over the 6 days following eclosion. Ten female wasps from each treatment were frozen daily and individually assayed. To compare with the capital nutrient as the initial baseline, nutrient level from 20 newly emerged female wasps (less than half hour old) was individually assayed. The levels of fructose, total sugars, glycogen, and total lipids in individual wasps were quantified using methods of van Handel (1985a, b) as adapted for parasitoids (Olson et al 2000, Fadamiro & Heimpel 2001, Lee et al 2004).

Statistical analyses

To compare the difference among different sugar diets on longevity, oogenesis, and nutrient content of parasitoids, one-way ANOVA complemented with least significant difference (LSD) test was used as all of raw data met assumptions of normality and homoscedasticity. All analyses were conducted in SAS software (version 9.0).

Results

Effect of five sugars on the longevity of *N. formosa*

The longevity of *N. formosa* fed on different sugars differed significantly ($F_{4, 119}=25.09$, $p<0.0001$). Longevity of wasps

fed on sugar was significantly longer, up to 6.5–9.3-fold than those wasps fed water only. The longevity of female wasps fed on glucose or sucrose were the longest, while those fed on melezitose was the shortest. There was no significant difference in longevity among females feeding on glucose, fructose, and sucrose ($F_{2, 59}=0.60$, $p>0.5541$) or between females fed on trehalose versus melezitose ($F_{1, 29}=0.02$, $p>0.8774$) (Table 1). Type II survivorship curves of wasps occurred in the six treatments. The survival peak was significantly prolonged by feeding on sugars, and the survival peak of wasps fed on glucose, fructose, or sucrose occurred significantly later than that of wasps fed on trehalose or melezitose (Fig 1).

Effect of five sugars on the oogenesis of *N. formosa*

A few (almost 6.0) mature eggs (rank III oocytes) existed in ovaries of newly emerged female wasps. In control treatment, mature oocytes were gradually reabsorbed. Meanwhile, the number of rank II oocytes increased within 24 h after eclosion and then decreased gradually to zero. The rank I oocytes increased during the first 24 h and remained relatively stable from 24–72 h after eclosion, and then decreased (Fig 2a).

The number of mature oocytes of the wasps provided with sugars significantly increased at first and then decreased compared with those wasps in control treatment. However, the timing of the peak of mature oocytes of their subsequent pattern varied between sugars, while the patterns of occurrence of immature (rank I and rank II) oocytes showed divergent patterns (Fig 2).

The number of mature oocytes in wasps provided with glucose peaked sharply at 24 h after eclosion (11.7 ± 2.1) and then decreased, remaining relatively stable; however, from 48–96 h. The number of rank II oocytes showed a double peaked curve and a concave appearance at 96 h. The number of rank I oocytes in wasps increased for the first 48 h and then decreased remaining relatively stable from 72 to 120 h (Fig 2b).

Similarly, when fructose was supplied, the number of mature oocytes peaked at 72 h (8.3 ± 1.1) and then decreased at 120 h. The number of rank II oocytes increased for the first 24 h, remained stable from 24–48 h, decreased after that, and then significantly increased at 96 h. The number of rank I oocytes increased for the first 24 h after eclosion, decreased

Table 1 The longevity of female *Neochrysocharis formosa* provided with five kinds of sugars (M±SE).

Food sources	Glucose	Fructose	Sucrose	Trehalose	Melezitose	Water
Longevity (days)	24.2±1.6A	21.8±1.1AB	23.7±2.0A	17.4±1.3BC	17.0±2.1C	2.6±0.2D

The different letters are statistically different at $p<0.05$ level according to ANOVA: LSD test.

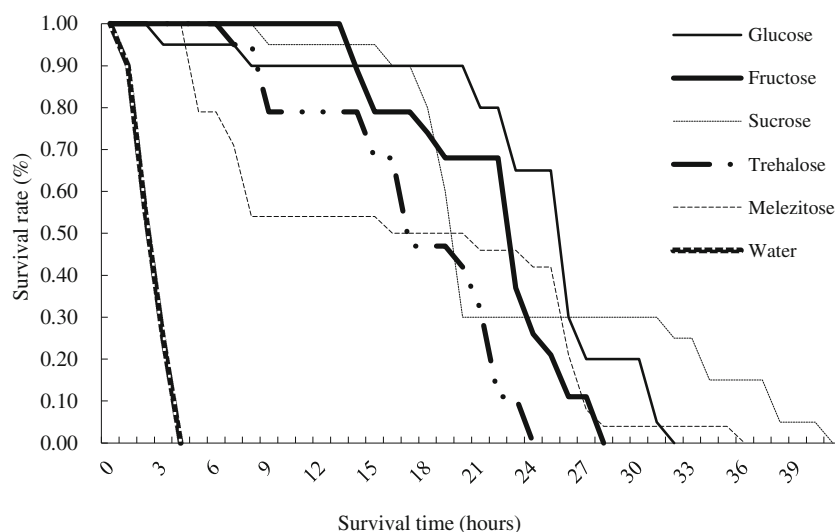


Fig 1 Survivorship curves for *Neochrysocharis formosa* provided with different sugars.

from 24–48 h, and then increased somewhat thereafter (Fig 2c).

However, when sucrose was supplied, the number of mature oocytes increased slightly for the first 24 h, increased significantly at 48 h, then it was relatively stable from 48–96 h with a peak at 72 h (7.8 ± 1.1), and then decreased sharply at 120 h. The number of rank II oocytes increased for the first 24 h, decreased slowly from 24–96 h, and then increased at 120 h. The number of rank I oocytes increased significantly for the first 24 h and then steadily increased from 24–72 h, decreased until 120 h and then increased (Fig 2d).

The number of mature oocytes in wasps provided with trehalose increased for the first 48 h with the peak (8.9 ± 1.2) at 48 h and then steadily decreased. The number of rank II oocytes increased significantly at 24 h, decreased significantly at 48 h, and then increased until it leveled out. The number of rank I oocytes increased significantly for the first 24 h, steadily decreased after that, but then reached a peak at 120 h (Fig 2e).

When melezitose was available, the number of mature oocytes decreased somewhat in the first 48 h, then increased at 72 h, and remained relatively stable from 72 to 96 h. It peaked (6.9 ± 0.5) at 96 h and then sharply decreased. The number of rank II oocytes increased significantly for the first 24 h, remained relatively stable during 24–48 h, decreased at 96 h, and then increased at 120 h. The number of rank I oocytes increased for the first 24 h and was relatively stable from 24 to 48 h, then increased until 72 h, and gradually decreased thereafter (Fig 2f).

While the maximum or peak value of daily average numbers of mature oocytes in the ovaries of female wasps among in the five sugars treatments were not significantly different ($F_{4, 49} = 2.12$, $p > 0.1934$), there was a significant difference between wasps provided with glucose and those provided with melezitose ($F_{1, 19} = 5.12$, $p < 0.0363$). The reciprocal

change pattern between the three types of oocytes (Fig 2) showed adult females had egg maturation and oosorption capability, and these were regulated by the nutrients they obtained.

Effect of five sugars on the nutrient content of *N. formosa* adults

In control treatment, the fructose content exhibited a slow, constant decline. Of other sugar treatments, the fructose content showed different patterns of abundance over time (Fig 3), reflecting the absorption and metabolic breakdown of the different sugars. Fructose content in wasps provided with glucose increased slowly for the first 72 h after emergence and then remained relatively stable; that in wasps provided with fructose generally showed an increasing tendency for the first 96 h and then rapidly decreased. The fructose contents in wasps provided with sucrose and melezitose showed an increasing tendency at first, with a peak at 24 and 72 h after emergence, respectively, and then slowly decreased; that in wasps provided with trehalose decreased for the first 48 h after emergence and then increased at a level lower than that in female adults at emergence.

The total sugar content of wasps in control treatment showed no change for the first 24 h after emergence but decreased rapidly thereafter. The total sugar content of wasps provided with glucose decreased somewhat in the first 24 h, then increased to the original level (at emergence), and then decreased again. Wasps provided with fructose increased slightly for the first 24 h, then slowly decreased until 144 h, and then rapidly decreased after that, but their total sugar content was higher than that in female wasps provided with glucose at the same stage. Total sugar content of wasps provided with sucrose, trehalose, and melezitose generally increased at first and then decreased, with peaks at 96, 24, and 48 h, respectively (Fig 4).

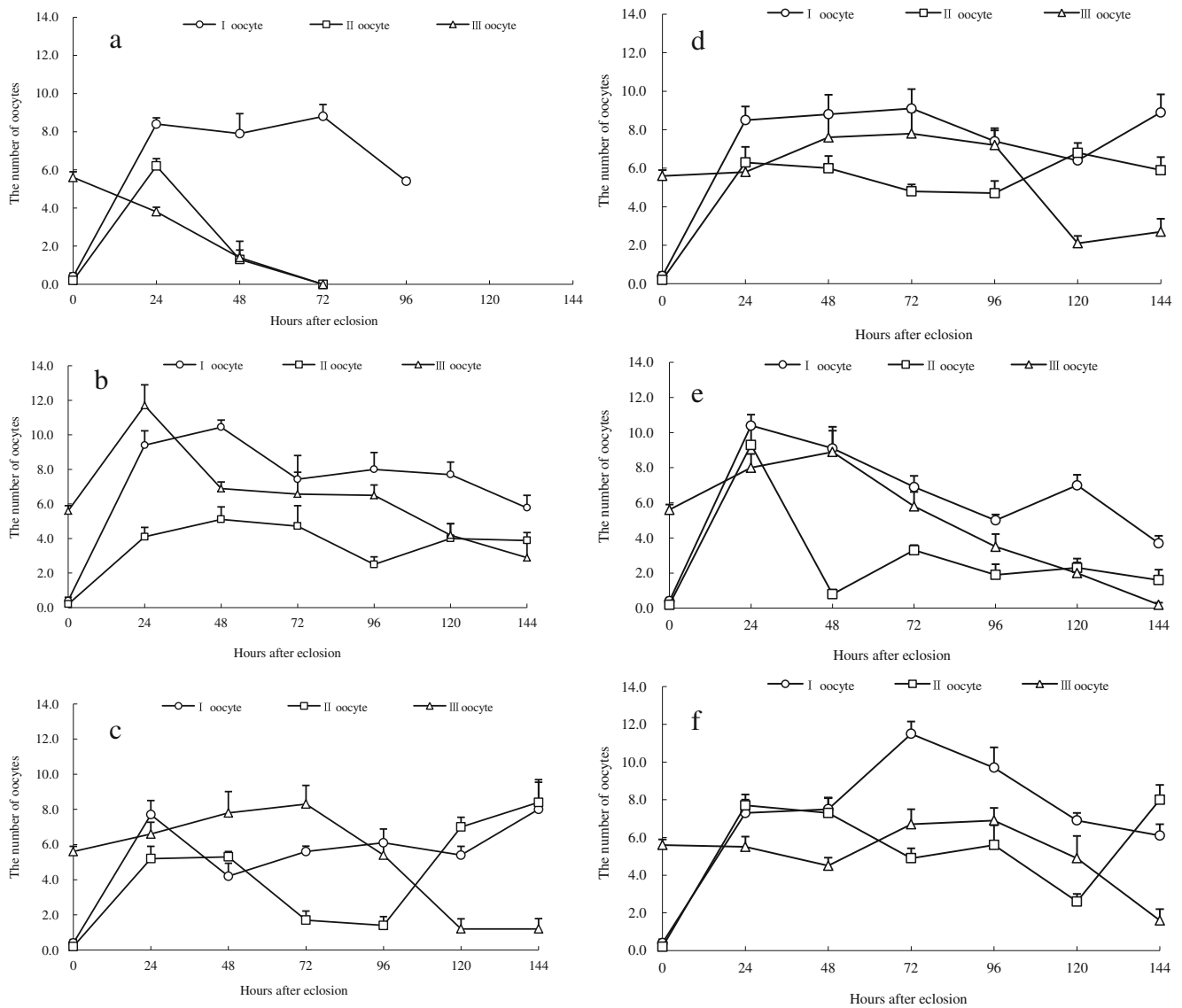
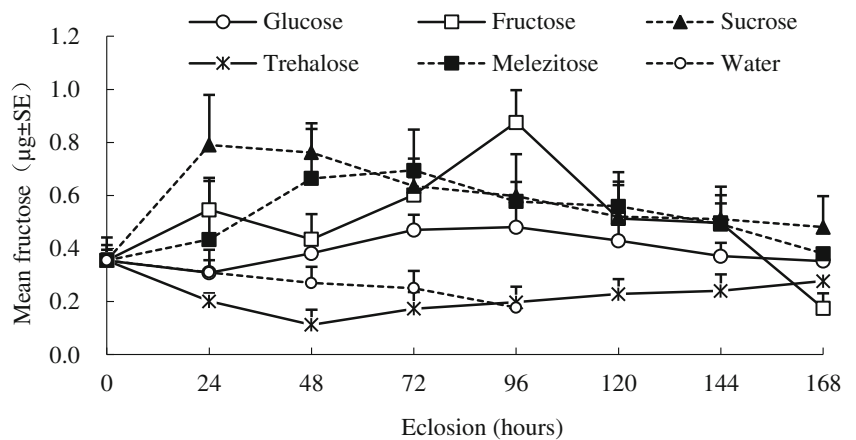


Fig 2 The occurrence dynamics of rank I, II, and III oocytes in female wasps provided with water (a), glucose (b), fructose (c), sucrose (d), trehalose (e), and melezitose (f).

Fig 3 Fructose content (micrograms) in female adults of *Neochrysocharis formosa* provided with different sugars (M±SE).



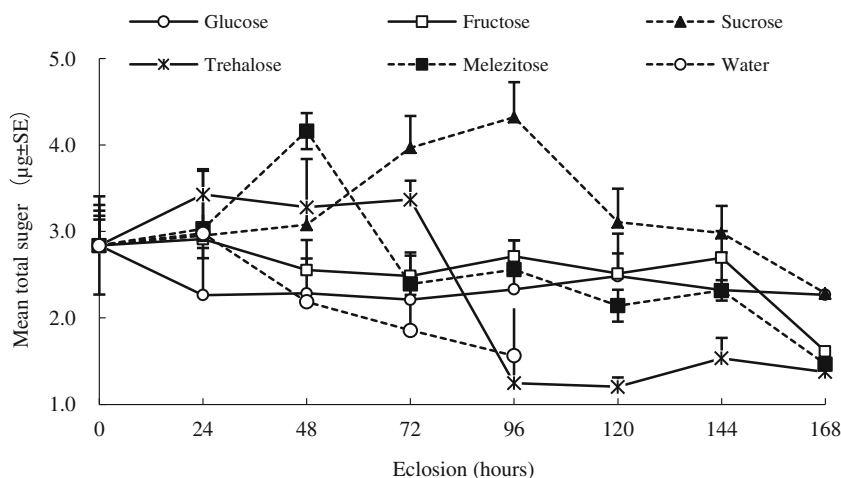


Fig 4 Total sugar content (micrograms) in female adults of *Neochrysocharis formosa* provided with different sugars (M±SE).

The glycogen content of wasps in control treatment rapidly decreased upon emergence. The glycogen content of wasps provided with the five sugars was at first higher and then lower than that in control individuals. Glycogen content of wasps provided with glucose increased at 24 h, decreased somewhat at 48 h, and then slowly increased again to the original level in newly emerged adults. The glycogen content in wasps provided with fructose remained relatively stable for the first 48 h, peaked at 72 h, and then decreased continuously, with the level lower at 120 h than that in individuals provided with glucose. The glycogen content of wasps provided with sucrose peaked at 48 h, decreased to their original levels at 72 h, increased slowly from 72–120 h, and then remained stable. The glycogen content of wasps provided with melezitose peaked at 24 h, decreased at 48 h, increased from 72–120 h, and then decreased to lower than the original level in the newly emerged adults. The glycogen content of wasps provided with trehalose peaked at 48 h, decreased sharply at 96 h, and then remained stable at a level lower than the original level (Fig 5).

The lipid content of wasps in control and the five sugars treatments all showed a decreasing trend (Fig 6). For the first

24 h after emergence, lipid content decreased most slowly in wasps provided with glucose and most quickly in wasps provided with fructose and sucrose. After that, the lipid content of wasps provided with fructose, sucrose, trehalose, and melezitose decreased at a slow speed, eventually reaching a stable level. At 168 h, wasps provided with glucose had the highest lipid content, followed by the wasps provided with sucrose, melezitose, trehalose, and fructose.

Discussion

Effect of sugars on female longevity

Neochrysocharis formosa is a larval endoparasitoid of agromyzid leafminers with destructive host feeding characteristics, which could suppress the host population not only by parasitization, but also by feeding on host larvae and stinging without oviposition and feeding (Chien & Ku 2001, Chien et al 2005, Moon et al 2004, Wang et al 2012a, Liu et al 2014, Zhang et al 2014).

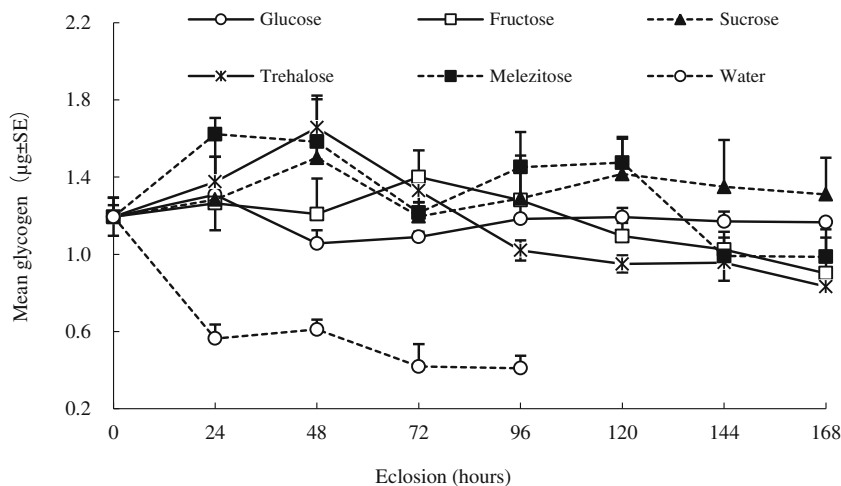


Fig 5 Glycogen content (micrograms) in female adults of *Neochrysocharis formosa* provided with different sugars (M±SE).

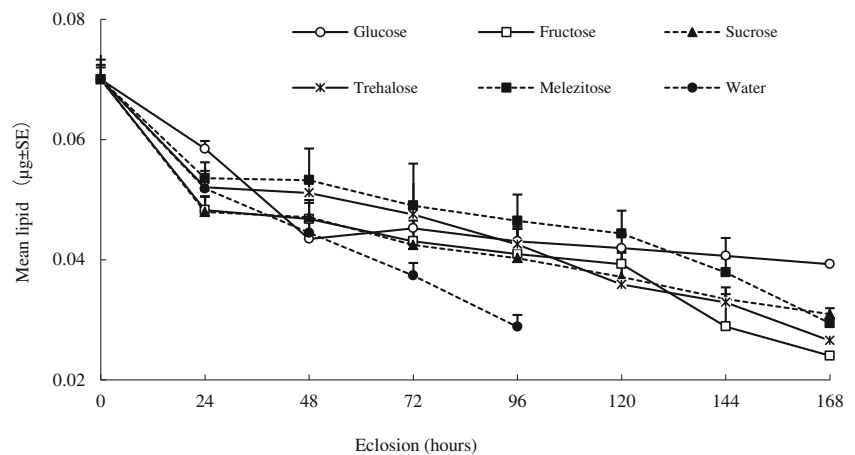


Fig 6 Lipid content (micrograms) in female adults of *Neochrysocharis formosa* provided with different sugars ($M \pm SE$).

Neochrysocharis formosa adult wasps can exploit the host larvae and the non-host food (such as nectar, honeydew, among others) as a food source (Chien & Ku 2001, Moon et al 2004, Song et al 2004). A previous study has shown that *N. formosa* provided with a honey solution had longer longevity and higher fecundity than that provided only with water, indicating that adult nutrition played an important role in oogenesis and longevity (Song et al 2004, 2005). Our results found that all five sugar diets can prolong wasp longevity to different extent.

The monosaccharide sugars tested (glucose and fructose) were similar or even superior to disaccharides and oligosaccharides, possibly because monosaccharides can be directly utilized by wasps, while disaccharides and oligosaccharides require hydrolysis before use. Oligosaccharide hydrolysis has a time lag, which resulted in the retarded absorption of nutrients and energy consumption (Wäckers 2001, Jervis et al 2008, Wang et al 2012b, Harvey et al 2012).

Most adult parasitoids cannot synthesize de novo lipids needed for oogenesis (Visser & Ellers 2008, Visser et al 2010); however, the capital lipids of adult wasps accumulated at the larval stage can be converted to compounds used for energy provision under nutrient stress (Jervis et al 2008, Arrese & Soulages 2010). Such use of capital nutrients may have partially obscured differences in effects on longevity of sugars tested, as would have digestion of tested sugars. For example, sucrose can easily be hydrolyzed to glucose and fructose, leading to little or no difference in effect on longevity by these two compounds (Table 1). However, females provided with trehalose and melezitose had decreased longevity, possibly because trehalose, as an insect hemolymph sugar, cannot exist in the body in high concentration (Jervis et al 2008). As a disaccharide, it can be absorbed only through hydrolysis to glucose. During the hydrolysis process, the metabolic energy consumption will result in the decreased longevity of female wasps. Similarly, melezitose can be absorbed only through hydrolysis to glucose and turanose, and then from turanose to glucose and fructose. During the hydrolysis of the turanose, the required energy

consumption may result in the decreased longevity of female wasps as well.

Different parasitoids vary in their capabilities for utilizing sugars (Ashley & Gonzales 1974, Leatemia et al 1995, McDougall & Mills 1997, Hirose et al 2009). For example, the five sugars tested in this study also had different effects on the longevity of *Diglyphus isaea* Walker, another strongly synovigenic parasitoid of agromyzid leafminers (Wang et al 2012b). The longevity of female *D. isaea* provided with fructose was significantly longer than that of those provided with glucose, disaccharide (sucrose and trehalose), and melezitose (Wang et al 2012b). Morales-Ramos et al (1996) found that the longevity of the synovigenic parasitoid *Catolaccus grandis* (Burks) fed on fructose and glucose was significantly longer than when fed on other food sources (amino acids and host hemolymph). Similar results were also found in *Trichogramma* parasitoids (Ashley & Gonzales 1974, Leatemia et al 1995, McDougall & Mills 1997). Hirose et al (2009) reported that the longevities of *Encarsia formosa* Gahan and *Eretmocerus eremicus* Rose & Zolnerowich were significantly prolonged when provided with glucose, fructose, and sucrose. But while trehalose did not prolong *E. formosa* longevity, it did for *E. eremicus*, due to the ability of these parasitoids in utilize this source of sugar. Wäckers (2001) also reported that *Microplectron fuscipennis* Zett. did not utilize melezitose to prolong its longevity, while *Cotesia glomerata* (L.) did. Both *N. formosa* and *D. isaea* can utilize melezitose, although the utilization efficiency for this sugar was lower than that for monosaccharides (glucose and fructose) and disaccharides (sucrose) (Wang et al 2012b).

Effect of sugars on oogenesis

The oogenesis and maturation of synovigenic female parasitoids need not only energy substances (e.g., sugars) but also lipids. The ovigeny index of *N. formosa* is 0.12, and the feeding of female wasps on host larvae can rapidly promote reproduction (Zhang et al 2014). We found that a few mature

oocytes are present in newly emerged female wasps, and egg maturation and oosorption of the female wasps can be regulated by nutrient intake. Oosorption capability and pattern (whether parasitoids prefer to absorb mature or nearly mature oocytes) were inconsistent with the general rule that had been found in female host-feeding parasitoids and some synovigenic non-host-feeding species during periods of host and/or food scarcity up to now (Bell & Bohm 1975, Jervis & Kidd 1986, Ralec 1995, Heimpel & Collier 1996). Regardless of the trigger for reabsorption or the ultimate destination of the reabsorbed materials, egg reabsorption serves to re-allocate resources in response to a change in habitat richness (Rivero & Casas 1999, Rosenheim *et al* 2000).

Lipids are the most important and indispensable resources for oogenesis and maturation in female parasitoids. The dynamics of lipid content can confirm that *N. formosa* cannot synthesize lipids from carbohydrates (Fig 6), which was similar to most parasitoids (Visser & Eilers 2008, Visser *et al* 2010). The number of mature oocytes in female wasps provided with sugars generally increased significantly at first (when sugars protected capital lipids from use as fuel sources), but then decreased, which is consistent with conclusions drawn by Heimpel *et al* (1997) and Rivero & Casas (1999).

The timing of maximum mature eggs in the ovaries of *N. formosa* females varied among the five sugars. Wasps provided with glucose rapidly formed more mature eggs because of the direct use of glucose as a fuel. In lipid synthesis from capital stores, glucose rather than fructose is needed, so the peak timing of development of new mature oocytes in female wasps provided with fructose lags behind wasps fed on glucose. The time needed for disaccharide oligosaccharide to be hydrolyzed to glucose resulted in the lag of the peak time of mature oocytes. The mature oocytes were rapidly reabsorbed due to the consumption of capital nutrients, and the oosorption facilitated prolonged longevity of female wasps and better adjustment to the environment (Bell & Bohm 1975, Papaj 2000, Richard & Casas 2009, Liu *et al* 2014). This study also revealed that some immature oocytes existed in the female wasps until death, so, if host food such as leafminer larvae were available, the female wasps could utilize the lipids in the host larvae to rapidly form new mature oocytes.

Effect of different sugars on nutrients in *N. formosa*

Our biochemical measurements showed that *N. formosa* was able to make good use of all five sugar resources. The longevity of female wasps was comprehensively determined by the absorption and accumulation capabilities of the sugars, the resulting compensation and regulation of capital nutrients, and the regulation of oogenesis. Synovigenic parasitoids tend to be flexible in their egg production, and they have wide scope for adjusting their life expectancy by their use of materials obtained from food, stored reserves, and, in

some species, their own eggs (Jervis & Kidd 1986, Jervis *et al* 2008). Therefore, different sugars may have varying effects on different synovigenic parasitoid wasps. Our results also showed that the female wasps have a weak ability to convert glucose to fructose. The dynamics of total sugar content and glycogen content in female wasps provided with monosaccharides (glucose and fructose) was relatively stable, while those in female wasps provided with disaccharides (sucrose and trehalose) and oligosaccharides (melezitose) varied significantly, suggesting that the female wasps directly use the monosaccharides but store the disaccharides as glycogen.

In this study, no host larvae were provided to the female wasps; hence, the decrease in the lipid content acquired from the pre-mature stage may not result from the oviposition loss, but the consumption during the conversion of lipids to oogenesis. The lipid content decreased due to the energy consumption during the formation of mature oocytes of female wasps, but at a slower speed, with an increase in number of oocytes in ovaries and in the speed of oocyte formation when they consumed rich sugars, which decreased their need for lipids. The rate of degradation of lipids differed with how different sugars provided energy, and this variation created a time lag. For example, the highest lipid content occurred at 144 h after the female wasps were provided with glucose.

This study showed that the complement of non-host nutrients provide energy for body maintenance, mitigate the degradation of lipids among capital nutrients, and enhance the efficiency of conversion of lipids to oocytes. However, the differences between sugars in hydrolysis and absorption capacity affected longevity and oogenesis. The fact that *N. formosa* was able to utilize all five sugars indicates that the wasp is able to exploit a wide variety of sugar resources in the field. Complementing the exogenous nutrients in the artificial rearing of *N. formosa* or planting nectar plants may therefore be effective means of enhancing the control efficiency of this parasitoid. Based on the longevity, oogenesis, and nutrient utilization of the wasps provided with the five sugar sources, glucose was the best sugar source.

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References

- Arrese EL, Soulages JL (2010) Insect fat body: energy, metabolism, and regulation. *Annu Rev Entomol* 55:207–225
- Ashley TR, Gonzales D (1974) Effect of various food substances on longevity and fecundity of *Trichogramma*. *Environ Entomol* 3:169–171

- Baker HG, Baker I (1983) Floral nectar sugar constituents in relation to pollinator type. In: Jones CE, Little RJ (eds) Handbook of experimental pollination biology. Van Nostrand Reinhold, New York, pp 117–141
- Bell WJ, Bohm MK (1975) Oosorption in insects. *Biol Rev* 50:373–396
- Bugg RL, Ellis RT, Carlson RW (1989) Ichneumonidae (Hymenoptera) using extrafloral nectar of faba bean (*Vicia faba* L., Fabaceae) in Massachusetts. *Biol Agric Hortic* 6:107–114
- Casas J, Pincebourde S, Mandon N, Vannier F, Poujol R, Giron D (2005) Lifetime nutrient dynamics reveal simultaneous capital and income breeding in a parasitoid. *Ecology* 86:545–554
- Chen L, Fadamiro HY (2006) Comparing the effects of five naturally occurring monosaccharide and oligosaccharide sugars on longevity and carbohydrate nutrient levels of a parasitic phorid fly, *Pseudacteon tricuspis*. *Physiol Entomol* 31:46–56
- Chien CC, Ku SC (2001) Instar preference of five species of parasitoids of *Liriomyza trifolii* (Hymenoptera: Eulophidae, Braconidae). *Formos Entomol* 21:89–97 (in Chinese)
- Chien CC, Ku SC, Chang SC (2005) Study of the storage and oviposition-regulating capability of *Neochrysocharis formosa* (Hymenoptera: Eulophidae). *Plant Prot Bull* 47:213–227 (in Chinese)
- Fadamiro HY, Heimpel GE (2001) Effects of partial sugar deprivation on lifespan and carbohydrate mobilization in the parasitoid *Macrocentrus grandii* (Hymenoptera: Braconidae). *Ann Entomol Soc Am* 94:909–916
- Flanders SE (1950) Regulation of ovulation and egg disposal in the parasitic Hymenoptera. *Can Entomol* 82:134–140
- Giron D, Rivero A, Mandon N, Darroutzet E, Casas J (2002) The physiology of host-feeding in parasitic wasps: implications for survival. *Funct Ecol* 16:750–757
- Giron D, Pincebourde S, Casas J (2004) Lifetime gains of host-feeding in a synovigenic parasitic wasp. *Physiol Entomol* 29:436–442
- Harvey JA, Cloutier J, Visser B, Ellers J, Wackers FL, Gols R (2012) The effect of different dietary sugars and honey on longevity and fecundity in two hyperparasitoid wasps. *J Insect Physiol* 58:816–823
- Heimpel GE, Collier TR (1996) The evolution of host-feeding behaviour in insect parasitoids. *Biol Rev* 71:373–400
- Heimpel GE, Rosenheim JA (1998) Egg limitation in parasitoids: a review of the evidence and a case study. *Biol Control* 11:160–168
- Hirose Y, Mitsunaga T, Yano E, Goto C (2009) Effects of sugars on the longevity of adult females of *Eretmocerus eremicus* and *Encarsia formosa* (Hymenoptera: Aphelinidae), parasitoids of *Bemisia tabaci* and *Trialeurodes vaporariorum* (Hemiptera: Aleyrodidae), as related to their honeydew feeding and host feeding. *Appl Entomol Zool* 44:175–181
- Idris AB, Grafius E (1995) Wildflowers as nectar sources for *Diadegma insulare* (Hymenoptera: Ichneumonidae) a parasitoid of diamondback moth (Lepidoptera: Yponomeutidae). *Environ Entomol* 24:1726–1735
- Jervis MA, Ferns PN (2004) The timing of egg maturation in insects: ovigeny index and initial egg load as measures of fitness and of resource allocation. *Oikos* 107:449–460
- Jervis M, Ferns P (2011) Towards a general perspective on life-history evolution and diversification in parasitoid wasps. *Biol J Linn Soc* 104:443–461
- Jervis MA, Kidd NAC (1986) Host-feeding strategies in hymenopteran parasitoids. *Biol Rev* 61:395–434
- Jervis MA, Kidd NAC, Fitton MG, Huddleston T, Dawah HA (1993) Flower-visiting by hymenopteran parasitoids. *J Nat Hist* 27:67–105
- Jervis MA, Heimpel GE, Ferns PN, Harvey JA, Kidd NAC (2001) Life-history strategies in parasitoid wasps: a comparative analysis of 'ovigeny'. *J Anim Ecol* 70:442–458
- Jervis MA, Ellers J, Harvey JA (2008) Resource acquisition, allocation, and utilization in parasitoid reproductive strategies. *Annu Rev Entomol* 53:361–385
- Leatemia JA, Laing JE, Corrigan JE (1995) Effects of adult nutrition on longevity fecundity and offspring sex ratio of *Trichogramma minutum* Riley (Hymenoptera Trichogrammatidae). *Can Entomol* 127:245–254
- Lee JC, Heimpel GE, Leibe GL (2004) Comparing floral nectar and aphid honeydew diets on the longevity and nutrient levels of a parasitoid wasp. *Entomol Exp Appl* 111:189–199
- Liu WX, Wang W, Cheng LS, Guo JY, Wan FH (2014) Contrasting patterns of ovarian development and oogenesis in two sympatric host-feeding parasitoids, *Diglyphus isaea* and *Neochrysocharis formosa* (Hymenoptera: Eulophidae). *Appl Entomol Zool* 49:305–314
- Luo SP, Li JC, Liu XX, Lu ZY, Pan WL, Zhang QW, Zhao ZW (2010) Effects of six sugars on the longevity, fecundity and nutrient reserves of *Microplitis mediator*. *Biol Control* 52:51–57
- McDougall SJ, Mills NJ (1997) The influence of hosts, temperature and food sources on the longevity of *Trichogramma platneri*. *Entomol Exp Appl* 83:195–203
- Moon HC, Jeon YK, Choi SW, Jeong SS, Ryu JO, Choi JS, Choi YG, Hwang CY (2004) Oviposition and host feeding characteristics of *Neochrysocharis formosa* (Hymenoptera: Eulophidae), an endoparasitoid of *Liriomyza trifolii* (Diptera: Agromyzidae). *Korean J Appl Entomol* 43:21–26
- Morales-Ramos JA, Rojas MG, King EG (1996) Significance of adult nutrition and oviposition experience on longevity and attainment of full fecundity of *Catolaccus grandis* (Hymenoptera: Pteromalidae). *Ann Entomol Soc Am* 89:555–563
- Olson DM, Fadamiro HY, Lundgren JG, Heimpel G (2000) Effects of sugar feeding on carbohydrate and lipid metabolism in a parasitoid wasp. *Physiol Entomol* 25:17–26
- Papaj DR (2000) Ovarian dynamics and host use. *Annu Rev Entomol* 45:423–448
- Ralec AL (1995) Egg contents in relation to host-feeding in some parasitic Hymenoptera. *Entomophaga* 40:87–93
- Richard R, Casas J (2009) Stochasticity and controllability of nutrient sources in foraging: host-feeding and egg resorption in parasitoids. *Ecol Monogr* 79:465–483
- Rivero A, Casas J (1999) Incorporating physiology into parasitoid behavioral ecology: the allocation of nutritional resource. *Res Pop Ecol* 41:39–45
- Rosenheim JA, Heimpel GE, Mangel M (2000) Egg maturation, egg resorption and the costliness of transient egg limitation in insects. *Proc R Soc London* 267B:1565–1573
- Saleh A, Allawi TF, Ghabeish I (2010) Mass rearing of *Neochrysocharis formosa* (Westwood) (Eulophidae: Hymenoptera), a parasitoid of leafminers (Agromyzidae: Diptera). *J Pest Sci* 83:59–67
- Shea K, Nisbet RM, Murdoch WW, Yoo HJS (1996) The effect of egg limitation on stability in insect host-parasitoid models. *J Anim Ecol* 65:743–755
- Song LQ, Gao Y, Xu ZF, Gu DJ (2004) Study on parasitic and reproductive characteristics of *Chrysonotomyia formosa* (Westwood). *Nat Enemies Insects* 26:113–121 (in Chinese)
- Song LQ, Gao Y, Zhang WQ, Gu DX, Xu ZF, Gu DJ (2005) Bionomics of *Chrysonotomyia formosa* (Westwood) (Hymenoptera: Eulophidae). *Acta Entomol Sin* 48:90–94 (in Chinese)
- Tompkins JML, Wratten SD, Wackers FL (2010) Nectar to improve parasitoid fitness in biological control: does the sucrose:hexose ratio matter? *Basic Appl Ecol* 11:264–271
- van Alphen JJM, Jervis MA (1996) Foraging behavior. In: Jervis MA, Kidd NAC (eds) *Insect natural enemies*. Chapman and Hall, London, pp 1–62
- van Handel E (1985a) Rapid determination of glycogen and sugars in mosquitoes. *J Am Mosq Control Assoc* 1:299–301
- van Handel E (1985b) Rapid determination of total lipids in mosquitoes. *J Am Mosq Control Assoc* 1:302–304
- van Handel E, Haeger JS, Hansen CW (1972) The sugars of some Florida nectars. *Am J Bot* 59:1030–1032
- Visser B, Ellers J (2008) Lack of lipogenesis in parasitoids: a review of physiological mechanisms and evolutionary implications. *J Insect Physiol* 54:1315–1322
- Visser B, Ellers J (2012) Effects of a lipid-rich diet on adult parasitoid income resources and survival. *Biol Control* 60:119–122

- Visser B, Lann CL, den Blanken FJ, Harvey JA, van Alphen JJM, Ellers J (2010) Loss of lipid synthesis as an evolutionary consequence of a parasitic lifestyle. *PNAS* 107:8677–8682
- Wäckers FL (2001) A comparison of nectar-and honeydew sugars with respect to the utilization by the hymenopteran parasitoid *Cotesia glomerata*. *J Insect Physiol* 47:1077–1084
- Wäckers FL, Björnson A, Dorn S (1996) A comparison of flowering herbs with respect to their nectar accessibility for the parasitoid *Pimpla turionellae*. *Proc Exp Appl Entomol* 7:177–182
- Wang W, Wang WX, Liu WX, Cheng LS, Wan FH (2012a) Research advances on biological characteristics and application of *Neochrysocharis formosa* (Westwood) (Hymenoptera: Eulophidae). *Chin J Biol Control* 28:575–582 (in Chinese)
- Wang W, Liu WX, Cheng LS, Wan FH (2012b) Effects of feeding different sugars on longevity and oogenesis in female adults of the synovigenic parasitoid *Diglyphus isaea* (Hymenoptera: Eulophidae). *Acta Entomol Sin* 55:964–970 (in Chinese)
- Zhang YB, Lu SL, Wang WX, Liu WX, Wang W, Wan FH (2014) Comparing immature development and life history traits in two coexisting host-feeding parasitoids, *Diglyphus isaea* and *Neochrysocharis formosa* (Hymenoptera: Eulophidae). *J Integrat Agric*, doi:10.1016/S2095-3119(14)60868-6