Demography and parasitic effectiveness of *Aphelinus asychis* reared from *Sitobion avenae* as a biological control agent of *Myzus persicae* reared on chili pepper and cabbage

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HIGHLIGHTS

- We used wheat as a host plant to rear *Sitobion avenae* to rear *Aphelinus asychis* to control *M. persicae*.
- The life history and life table parameters of *A. asychis* parasitizing and feeding on *M. persicae* on chili pepper and cabbage were compared.
- The parasitoids performed better in development, fecundity, longevity, and nutritional feeding on *M. persicae* reared on chili pepper than that on cabbage.
- *Aphelinus asychis* reared from *S. avenae* was a better biological control agent of *M. persicae* on chili pepper than on cabbage.

GRAPHICAL ABSTRACT
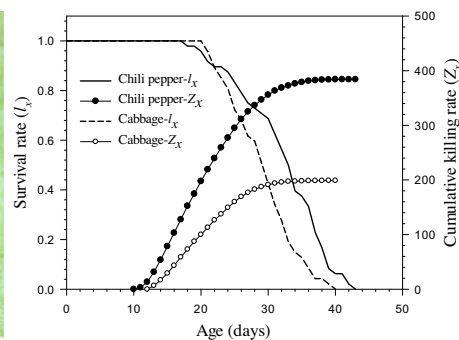
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ABSTRACT

To develop a bank plant system for the biological control of vegetable aphids, we used wheat, *Triticum aestivum* L., as a host plant to rear the English grain aphid, *Sitobion avenae* Fabricius, as an alternative host for rearing the parasitoid *Aphelinus asychis* Walker. *A. asychis* reared from *S. avenae* were allowed to parasitize second instar *Myzus persicae* nymphs feeding on chili pepper and cabbage plants. We compared the life history and life table parameters of *A. asychis*, including development time, pupal mortality, sex ratio, longevity, fecundity and host-feeding of the F_1 generation. The data were analyzed using the age-stage, two-sex life table method. We found that the parasitoids reared from *S. avenae* could successfully parasitize and host-feed *M. persicae* on chili pepper and cabbage, but they performed differently when the aphids on the two host plants were offered. The parasitoids had a shorter developmental duration, higher proportion of female progeny, longer longevity, higher fecundity and feeding rate when parasitizing the aphids on chili pepper than on cabbage. Based on the life table parameters, the including intrinsic rate of increase (r), net reproductive rate (R_0) and net aphid killing rate (Z_0), *A. asychis* reared from *S. avenae* performed better as a biological control agent of *M. persicae* on chili pepper than on cabbage.

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1. Introduction

Chili pepper (*Capsicum annuum* L., Solanaceae) and cabbage (*Brassica oleracea* L., Brassicaceae) are two important vegetables planted in greenhouses and open-air fields in China (Wang et al., 2013, 2014). The green peach aphid, *Myzus persicae* Sulzer (Hemiptera: Aphididae), is considered as one of the most important pests infesting vegetable crops, including chili pepper and cabbage (Blackman and Eastop, 1985), due to its very rapid population increase, wide host range and high insecticide resistance (Yano, 2003). *M. persicae* causes great losses in yield and quality of the products and acts indirectly as a vector of viral diseases (Castle and Berger, 1993; Syller, 1994). Over the last decade, insecticides have been the most common method used for controlling *M. persicae*. However, the extensive use of insecticides has resulted in increasing insecticide resistance and in decreasing populations of natural enemies (van Emden et al., 2014). As the danger of pesticides was realized, the biological control of insect pests, including *M. persicae* and other aphid species, has been adopted worldwide.

Using a banker plant system to carry natural enemies to control pests was first reported by Starý (1970) and has been extensively studied and widely used in recent years worldwide (Frank, 2010; Xiao et al., 2011a,b). It consists of a plant that directly or indirectly provides resources, such as food or raising prey, for natural enemies that are deliberately released into a cropping system (Frank, 2010; Xiao et al., 2011a,b). The banker plant system uniquely combines the advantages of both augmentative and conservation biological controls, providing preventative, long-term suppression of arthropod pests (Xiao et al., 2012). Therefore, the development of a banker plant system for managing aphids has increasingly become an alternative option for the biological control of pests, especially under protected cropping systems (Frank, 2010; Ohta and Honda, 2010; Andorno and López, 2014). However, natural enemies must be introduced into greenhouses immediately after the appearance of pests on crops because a late release will result in unsuccessful control (Nagasaka and Oya, 2003; Yano, 2003; Ohta and Honda, 2010).

Among the parasitoids for aphid control, *Aphelinus* (Hymenoptera: Aphelinidae) and *Aphidius* (Hymenoptera: Aphidiidae) have been widely used in both greenhouse and field production environments, especially *Aphelinus asychis* Walker (Hymenoptera: Aphelinidae) (van Emden, 1995, 2014), which is a polyphagous endoparasitoid (Byeon et al., 2011a,b) capable of parasitizing and host-feeding on approximately 40 aphid species, including *M. persicae* (Li et al., 2007). This species is native to most parts of the eastern hemisphere, such as Europe, Asia, and Africa (Bai and Mackauer, 1990a), and has potential as a biological control candidate for *M. persicae* (Sulzer) (Takada, 2002; Tatsumi and Takada, 2005).

To establish a non-crop banker plant system employing the parasitoid *A. asychis*, we selected wheat (*Triticum aestivum* L.) to rear the English grain aphid, *Sitobion avenae* (Hemiptera: Aphididae), as an alternative host for the parasitoid for the biological control of *M. persicae* on various vegetables in greenhouses. However, we lacked detailed knowledge on the biological and ecological characteristics of *A. asychis* after switching the host from *S. avenae* to *M. persicae*, and there were no previous reports in the literature. Therefore, our overall goal in this study was to evaluate the development duration, survival rate, sex ratio, longevity, age-specific fecundity, age-specific feeding rate, age-specific non-effective parasitism rate, and age-specific aphid killing rate of the first generation of *A. asychis* originating from *S. avenae* reared on wheat to parasitize and host-feed *M. persicae* infesting chili pepper and cabbage plants. This information will be useful for using the wheat-*S. avenae*-*A. asychis* system to control *M. persicae* on chili pepper and cabbage.

2. Materials and methods

2.1. Insects and plants

M. persicae, *S. avenae* and *A. asychis* were originally collected from the greenhouses of the Key Laboratory of Applied Entomology, Northwest A&F University (Yangling, Shaanxi, China) in 2013. The aphids and parasitoids were maintained in air-conditioned insectaries [25 ± 2 °C, 70 ± 10% RH, with a photoperiod of 14:10 (L:D) h]. *M. persicae* were reared on chili pepper (var. 'Ox horn') and white cabbage (var. 'Qingan 80') plant. The aphid parasitoid (11 generations) *A. asychis* emerged from mummified *S. avenae* reared on wheat (var. 'Xinong 979'). Chili pepper, cabbage and wheat plants were grown in 12 cm diameter plastic pots filled with soil mix (peat moss: perlite = 3:1) and enclosed in nylon net cages (60 × 60 × 60 cm^3). The plants were watered and fertilized (Compost, COMPO Expert GmbH, Münster-Handorf, Germany) as needed.

2.2. Life tables and predation

Chili pepper (~120 days old) and cabbage (~80 days old) were used as the host plants for *M. persicae*. Three milliliters of water-agar (1%) was trickled into a petri dish (3 cm diameter). After refrigeration, the leaf discs (3 cm diameter) of chili pepper or cabbage were individually placed on the agar gel surface in the petri dish. Then, 30 *M. persicae* adults reared on chili pepper or cabbage plants were placed into each petri dish on the leaf disc, respectively, and allowed to feed and reproduce. After 24 h, those aphid adults were removed, and the newborn nymphs remained on the leaf disc for after another 24 h. Newly molted second instar nymphs (~100) were used in the experiments, and all younger nymphs and the ecdyses were removed. Five mated female adults of *A. asychis* that emerged from *S. avenae* were introduced into a petri dish using an aspirator. After 24 h, the parasitoid adults were removed. The petri dishes with both parasitized and unparasitized aphids were maintained in an incubator at 25 ± 0.5 °C, 70 ± 10% RH, and a photoperiod of 14: 10 (L:D) h, and all aphids were allowed to develop until the parasitized aphids mummified. The aphids that were not mummified were removed using a hairbrush. Fifty mummies were randomly selected from each petri dish, and the rest were removed. In preliminary experiments, we dissected aphids and found that when the color of parasitized aphids turned to black for 24 h, the parasitoid larva had developed into a pupa. The pupal stage was considered from pupa formation until adult emergence. The development of all mummies was monitored and recorded until the parasitoids emerged as adults or died. The emerged female and male adults of *A. asychis* were paired. Thirty-four and thirty-six pairs of parasitoids were used for cabbage and chili pepper, respectively. One couple was introduced into a petri dish with 50 2nd instar aphids, and the female was allowed to oviposit and feed for 24 h. The parasitoids were transferred daily to a new petri dish with 50 aphids on the leaf disc of either chili pepper or cabbage. This process was continued until the female parasitoid died. A new male was provided if the male died before the female. After removal of the parasitoids, the aphids were separately placed in growth chambers and observed daily for mummies and the emergence of parasitoid offspring. The survival, aphids consumed for nutrition, daily mummified aphids, and successfully emerged parasitoid offspring were recorded daily.

2.3. Life table analysis

The raw data on development, survival rate, longevity and daily fecundity (effective parasitism) of individual *A. asychis* females

were analyzed according to the age-stage, two-sex life table (Chi and Liu, 1985; Chi, 1988) using a computer program TWOSEX-MSChart (Chi, 2015b). Data on daily feeding rate, non-effective parasitism rate and aphid killing rate were analyzed using the computer program CONSUME-MSChart (Chi, 2015a). Following Chi and Liu (1985), the age-stage-specific survival rate (s_{xj}) (x = age, j = stage), age-specific survival rate (l_x), age-stage-specific fecundity (f_{xj}), age-specific fecundity (m_x), net reproductive rate (R_0), intrinsic rate of increase (r), finite rate of increase (λ), and mean generation time (T) were calculated. In the age-stage, two-sex life table, the age-specific fecundity (m_x) is calculated as

$$m_x = \frac{\sum_{j=1}^{\beta} s_{xj} f_{xj}}{\sum_{j=1}^{\beta} s_{xj}}$$

where β is the number of life stages. For a parasitoid, the age-stage fecundity f_{xj} is actually the effective parasitism rate, i.e., the number of parasitoids that successfully emerge from mummified aphids. The cumulative reproductive rate (R_x) is the number of offspring produced by a female from birth to age x, while the net reproductive rate (R_0) is the total offspring produced by a female during its lifetime, which were calculated according to Chi and Su (2006) as follows:

$$R_x = \sum_{i=0}^{x} l_i m_i \quad \text{and} \quad R_0 = \sum_{x=0}^{\infty} l_x m_x = \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} s_{xj} f_{xj}$$

The intrinsic rate of increase (r) was estimated using the iterative bisection method and the Euler-Lotka equation with the age indexed from 0 (Goodman, 1982):

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1$$

The finite rate (λ) and the mean generation time (T) were calculated as follows:

$$\lambda = e^r$$

$$T = \frac{\ln(R_0)}{r}$$

The life expectancy (e_{xj}) was calculated according to Chi and Su (2006), while the reproductive value (v_{xj}) was calculated according to Huang and Chi (2011) and Tuan et al. (2014a,b).

2.4. Host-feeding data analysis

The feeding rate is the number of aphids killed by the parasitoids to obtain nutrition. The age-specific feeding rate (k_x) was calculated according to Chi and Yang (2003) and Yu et al. (2005) as follows:

$$k_x = \frac{\sum_{j=1}^{\beta} s_{xj} c_{xj}}{\sum_{j=1}^{\beta} s_{xj}}$$

where c_{xj} is the age-stage-specific feeding rate of individuals at age x and stage j. Accounting for the age-specific survival rate, the age-specific net feeding rate (q_x) was calculated as follows:

$$q_x = l_x k_x$$

The cumulative feeding rate (C_x) is the number of aphids killed by an average parasitoid from birth to age x, while the net feeding rate (C_0) is the total number of aphids killed by an average individual during its life span, and these values were calculated as follows:

$$C_x = \sum_{i=0}^{x} l_i k_i \quad \text{and} \quad C_0 = \sum_{x=0}^{\infty} l_x k_x = \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} s_{xj} c_{xj}$$

For a proper comparison of host-feeding potential, we incorporated both the finite rate and the feeding rate into the finite feeding rate according to Chi et al. (2011) and Yu et al. (2013). The finite feeding rate (ω) was calculated as follows:

$$\omega = \lambda \psi = \lambda \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} a_{xj} c_{xj}$$

where ψ is the stable feeding rate, and a_{xj} is the proportion of individuals belonging to age x and stage j in a stable age-stage distribution. The stable feeding rate was calculated as:

$$\psi = \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} a_{xj} c_{xj}$$

2.5. Non-effective parasitism rate analysis

The non-effective parasitism rate is defined as the number of aphids that a parasitoid successfully parasitized, but no parasitoid adult emerged from the mummies. The age-specific non-effective parasitism rate (g_x) was also calculated by the methods of Chi and Yang (2003) and Yu et al. (2005) as follows:

$$g_x = \frac{\sum_{j=1}^{\beta} s_{xj} d_{xj}}{\sum_{j=1}^{\beta} s_{xj}}$$

where d_{xj} was the age-stage-specific non-effective parasitism rate of individuals at age x and stage j. Again, when accounting for the age-specific survival rate, the age-specific non-effective parasitism rate (h_x) was calculated as follows:

$$h_x = l_x g_x$$

net

The cumulative non-effective parasitism rate (N_x) is the number of aphids killed by a parasitoid from birth to age x, while the net non-effective parasitism rate (N_0) is the total number of aphids killed by an individual during its life span, and these values were calculated as follows:

$$N_x = \sum_{i=0}^{x} l_i g_i \quad \text{and} \quad N_0 = \sum_{x=0}^{\infty} l_x g_x = \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} s_{xj} d_{xj}$$

For a comparison of the non-effective parasitism rate, we incorporated both the finite rate and the non-effective parasitism rate into the finite non-effective parasitism rate. The finite non-effective parasitism rate (ε) was calculated as follows:

$$\varepsilon = \lambda \gamma = \lambda \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} a_{xj} d_{xj}$$

where γ is the stable non-effective parasitism rate and was calculated as

$$\gamma = \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} a_{xj} d_{xj}$$

2.6. Killing rate analysis

The killing rate is defined as the number of aphids killed by a parasitoid through host-feeding, non-effective parasitism, and effective parasitism. The age-specific aphid killing rate (u_x) was calculated by the methods of Chi and Yang (2003) and Yu et al. (2005) as follows:

Table 1
Developmental periods and offspring of *Aphelinus asychis* feeding on *Myzus persicae* on chili pepper and cabbage.

Stage	Chili pepper			Cabbage		
	n	Mean ± SE	Range	n	Mean ± SE	Range
Egg + larva (d)	48	6.0 ± 0.1 a	5–8	47	6.8 ± 0.1 b	5–9
Pupa (d)	48	6.4 ± 0.1 a	6–8	47	6.7 ± 0.1 b	5–8
Preadult (d)	48	12.4 ± 0.2 a	11–16	47	13.5 ± 0.1 b	13–16
Female longevity (d)	36	35.3 ± 0.7 a	18–43	34	31.3 ± 0.7 b	12–27
Female adult longevity (d)	36	23.1 ± 0.6 a	15–30	34	17.8 ± 0.7 b	10–27
Male longevity (d)	12	23.7 ± 0.9 a	18–29	13	24.2 ± 0.8 a	21–30
Male adult longevity (d)	12	10.9 ± 0.8 a	6–14	13	10.9 ± 0.7 a	8–16
Oviposition period (d)	36	21.1 ± 0.6 a	14–30	34	16.0 ± 0.7 b	9–26
Offspring (egg/female)	36	414.6 ± 12.2 a	315–656	34	210.5 ± 11.2 b	76–435

Means in the same row followed by different letters denote significant differences between chili pepper and cabbage (100,000 Bootstraps, $P < 0.05$).

$$\mu_x = \frac{\sum_{j=1}^{\beta} s_{xj} P_{xj}}{\sum_{j=1}^{\beta} s_{xj}}$$

where p_{xj} is the age-stage-specific aphid killing rate of individuals at age x and stage j and is the summation of c_{xj}, d_{xj}, and f_{xj}, i.e., $p_{xj} = c_{xj} + d_{xj} + f_{xj}$. Accounting for the age-specific survival rate, the age-specific net aphid killing rate (w_x) was calculated as follows:

$$w_x = l_x u_x$$

The cumulative killing rate (Z_x) is the total number of aphids killed by a parasitoid from birth to age x, while the net killing rate (Z_0) is the total number of aphids killed by an individual during its life span, and these values were calculated as follows:

$$Z_x = \sum_{i=0}^{x} l_i u_i \text{ and } Z_0 = \sum_{x=0}^{\infty} l_x u_x = \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} s_{xj} p_{xj} = R_0 + C_0 + N_0$$

For an overall comparison of killing potential, we incorporated both the finite rate and the killing rate into the finite killing rate. The finite killing rate (θ) was calculated as follows:

$$\theta = \lambda\vartheta = \lambda \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} a_{xj} p_{xj}$$

where ϑ is the stable killing rate, calculated as

$$\vartheta = \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} a_{xj} p_{xj}$$

The transformation rate (Q_p) from aphid population to parasitoid offspring, representing the mean number of aphids a parasitoid needs to kill to produce one offspring, was calculated as follows:

$$Q_p = \frac{Z_0}{R_0} = \frac{R_0 + C_0 + N_0}{R_0}$$

2.7. Statistical analysis

The bootstrap technique was used to estimate the standard errors of the life history data, population parameters, feeding rates, non-effective parasitism rates and aphid killing rates (Efron and Tibshirani, 1993). Because the bootstrap technique uses random resampling, a small number of replications will generate highly variable standard errors. To obtain stable and precise results, we used 100,000 bootstraps in this study. We used the paired bootstrap test to compare the differences between treatments based on the confidence interval of the difference between treatments.

3. Results

3.1. Age-stage, two-sex life table

Of the 50 mummified aphids of *A. asychis* collected from each crop at the beginning of the life table study, 48 from the aphids on chili pepper and 47 from the aphids on cabbage pupated and successfully emerged as adults. The mean developmental duration of the pre-adult stages, longevity, and the female fecundity and oviposition period of *A. asychis* are given in Table 1. The longevity of an *A. asychis* female adult (23.1 d) reared on the aphids on chili pepper was 5 days longer than when reared on the aphids on cabbage (17.8 d). There was, however, no significant difference in male longevity between *A. asychis* that emerged from aphids reared on chili pepper and cabbage. The total number of offspring of *A. asychis* female adults reared on aphids on chili pepper was 414.6 eggs/female, which was twice the number on cabbage (210.5 eggs/female).

The age-stage survival curve s_{xj} depicts the probability that a newborn will survive to age x and stage j (Fig. 1). Overlaps between survival rates of different stages can be observed in Fig. 1. The number of offspring produced by individual female *A. asychis* at age x and stage j is shown by the curve f_{x3} (female adult is the third life stage) (Fig. 2). The curves of age-specific survival rate (l_x), age-specific fecundity (m_x), and age-specific maternity ($l_x m_x$) are also plotted in Fig. 2. When feeding on the aphids on cabbage and chili pepper, the curves of the age-stage-specific fecundities (f_{x3}) of the parasitoids reached peaks in reproduction at the 17th day and 15th day, respectively, and the values of f_{x3} were 16.7 offspring and 29.1 offspring, respectively. When feeding on the aphids reared on cabbage, the curves of m_x and $l_x m_x$ of the parasitoids showed peaks of 12.1 offspring at age 17 d, and the oviposition period was 16.0 d. The curves of m_x and $l_x m_x$ of *A. asychis* adult females reared on the aphids on chili pepper, reached higher peaks (21.4 offspring) at age 17 d, but the oviposition period on chili pepper was longer (21.1 d) than on cabbage.

3.2. Population parameters

The population parameters of *A. asychis* are listed in Table 2. The intrinsic rate of increase (r), finite rate of increase (λ), net reproduction rate (R_0), and mean generation time (T) of *A. asychis* feeding on the aphids on chili pepper were 0.3135 d^{-1}, 1.3682 d^{-1}, 310.9 offspring and 18.3 d, respectively. The values of r, λ, R_0, and T of *A. asychis* reared on aphids from cabbage were 0.2590 d^{-1}, 1.2957 d^{-1}, 152.3 offspring and 19.4 d, respectively. The population parameters of *A. asychis* reared on the aphids on chili pepper were significantly higher than on cabbage, while the mean generation time (T) of *A. asychis* feeding on the aphids on chili pepper was significantly shorter than on cabbage.
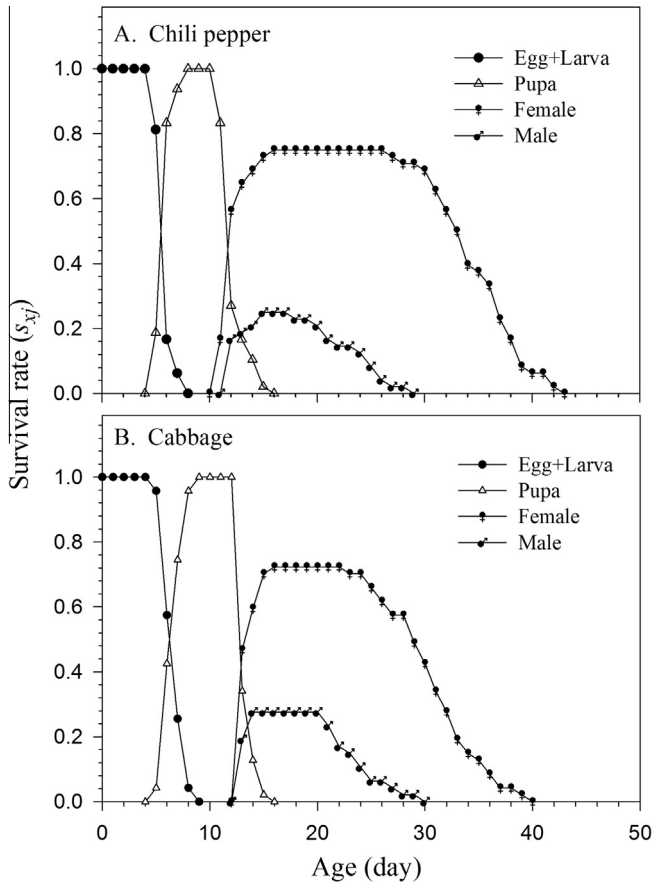
Fig. 1. The age-stage-specific survival rates (s_{xj}) of *Aphelinus asychis* parasitizing and feeding on *Myzus persicae* on chili pepper (A) and cabbage (B).

Fig. 2. Age-specific survival rates (l_x), fecundities (m_x), maternities (l_xm_x) and age-stage-specific fecundities (f_{x3}) of *Aphelinus asychis* parasitizing and feeding on *Myzus persicae* on chili pepper (A) and cabbage (B).

The life expectancy (e_{xj}) of each age-stage group of *A. asychis* is plotted in Fig. 3 and gives the time that individuals of age x and stage j could be expected to live after age x. For example, the life expectancy of a newborn egg of *A. asychis* preying on the aphids on chili pepper was 32.4 d, which was longer than on cabbage (29.3 d). The peak life expectancy (e_{xj}) of *A. asychis* female adults feeding on the aphids on chili pepper was 24.3 d at age 11 d, which was longer than the peak on cabbage (18.3 d) at age 13 d. Because this study was conducted in the laboratory without the adverse effects of field conditions, the life expectancy decreased gradually with age.

The contribution of an individual to the future population was defined as the reproductive value by Fisher (1930). The reproductive values (v_{xj}) of individuals at age x and stage j of *A. asychis* are presented in Fig. 4. The v_{xj} of *A. asychis* feeding on the aphids on chili pepper and cabbage had reproductive values of 1.3682 d^{-1} and 1.2957 d^{-1}, respectively, which was also the value of the finite rate of increase. Females near the peak of reproduction, however, contributed considerably more to the population than at other ages and stages. The peak reproductive value (v_{xj}) of an *A. asychis* female adult preying on the aphids on chili pepper was 98.9 d^{-1} at age 15 d, which was greater than 63.6 d^{-1} for feeding on the aphids on cabbage at age 16 d.

3.3. Feeding rate

The feeding rates of *A. asychis* are plotted in Fig. 5. Because *A. asychis* could not prey on aphids during the egg, larva, and pupa stages, these stages formed gaps in the feeding rate before adult emergence. Both the age-specific feeding rate (k_x) and the
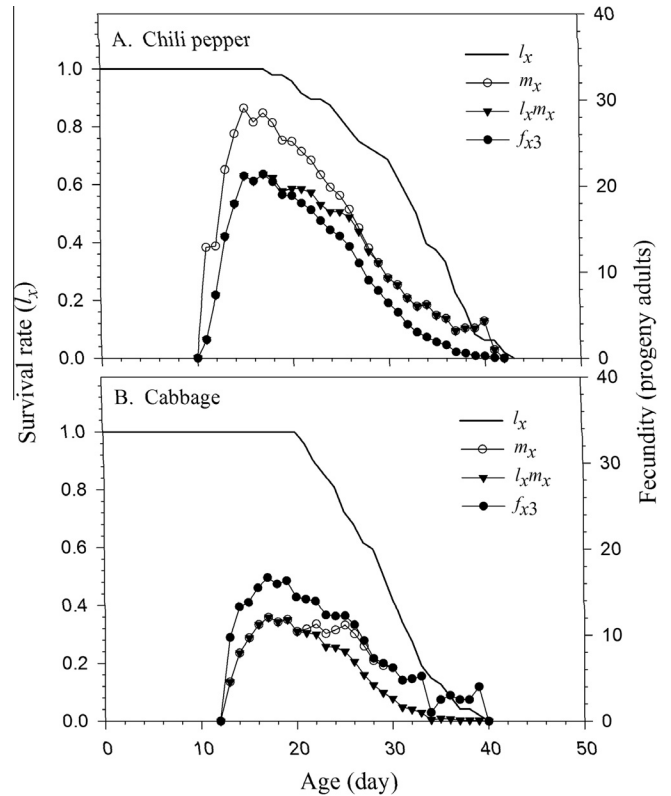
age-specific net feeding rate (q_x) of *A. asychis* feeding on the aphids on chili pepper and cabbage showed roughly periodic peaks during all adult female stages. The maximum daily age-specific feeding rate (k_x) of *A. asychis* preying on the aphids on chili pepper (2.8 aphids at age 13 d) was higher than on cabbage (2.3 aphids at age 16 d). The maximum daily age-specific net feeding rates (q_x) of *A. asychis* feeding on the aphids on chili pepper and cabbage were 2.8 aphids at age 13 d and 2.3 aphids at age 16 d, respectively, and the former is greater than the latter.

The net feeding rates were listed in Table 2. Because an *A. asychis* female adult feeding on the aphids on chili pepper lived longer, and taking survival rates, feeding rates, and longevity into consideration, the net feeding rate (C_0) of aphids killed by *A. asychis* on chili pepper was 46.5 aphids per individual, which was greater than on cabbage (29.8 aphids per individual).

The stable feeding rate (ψ) and finite feeding rate (ω) are listed in Table 2. The stable feeding rate and finite feeding rate of *A. asychis* feeding on the aphids on chili pepper (0.0645 and 0.0882, respectively) were not significantly different from the corresponding values on cabbage (0.0631 and 0.0817, respectively).

3.4. Non-effective parasitism rate

The non-effective parasitism rates of *A. asychis* are plotted in Fig. 6. Both the daily age-specific non-effective parasitism rate (g_x) and the daily age-specific net non-effective parasitism rate (h_x) of *A. asychis* feeding on the aphids on chili pepper and cabbage showed irregular periodic peaks during all adult female stages. The net non-effective parasitism rate (N_0) is listed in Table 2. Because the female adults of *A. asychis* feeding on the aphids on chili pepper lived longer, and taking survival rates, non-effective parasitism rates, and longevity into consideration, the value of N_0 of aphids

Table 2
Population parameters, feeding rate, non-effective parasitism rate and killing rate of *Aphelinus asychis* feeding on *Myzus persicae* on chili pepper and cabbage.

Parameter	Chili pepper	Cabbage
Intrinsic rate of increase, r (d^{-1})	0.3135 ± 0.0064 a	0.2590 ± 0.0059 b
Finite rate of increase, λ (d^{-1})	1.3682 ± 0.0088 a	1.2957 ± 0.0076 b
Net reproductive rate, R_0 (offspring)	310.9 ± 27.4 a	152.3 ± 15.9 b
Mean generation time, T (d)	18.3 ± 0.2 a	19.4 ± 0.2 b
Net feeding rate, C_0 (aphids)	46.5 ± 4.5 a	29.8 ± 3.0 b
Stable feeding rate, ψ	0.0645 ± 0.0058 a	0.0631 ± 0.0054 a
Finite feeding rate, ω	0.0882 ± 0.0084 a	0.0817 ± 0.0074 a
Net non-effective parasitism rate, N_0 (aphids)	26.4 ± 2.7 a	16.5 ± 2.6 b
Stable non-effective parasitism rate, ε	0.0250 ± 0.0025 a	0.0285 ± 0.0072 a
Finite non-effective parasitism rate, γ	0.0342 ± 0.0037 a	0.0369 ± 0.0094 a
Net killing rate, Z_0 (aphids)	384.1 ± 33.7 a	198.8 ± 20.5 b
Stable killing rate, θ	0.4594 ± 0.0378 a	0.3822 ± 0.0315 b
Finite killing rate, ϑ	0.6286 ± 0.0557 a	0.4952 ± 0.0436 b
Transformation rate, Q_p	1.2355 ± 0.0088 a	1.3054 ± 0.0139 b

Means in the same row followed by different letters denote significant differences between cabbage and chili pepper (Bootstrap, $p < 0.05$).

killed by *A. asychis* on chili pepper was 26.4 aphids per female adult, which was significantly greater than on cabbage (16.5 aphids). The stable non-effective parasitism rate and finite non-effective parasitism rate are listed in Table 2. The stable non-effective parasitism rate and finite non-effective parasitism rate of *A. asychis* feeding on the aphids on chili pepper (0.0250 and 0.0342, respectively) were not significantly different from the corresponding values on cabbage (0.0285 and 0.0369, respectively).

3.5. Aphid killing rate

The aphid killing rate is plotted in Fig. 7. The maximum age-specific aphid killing rate (u_x) of *A. asychis* preying on aphid nymphs on chili pepper was 25.3 aphids on the 18th day, which was higher than on cabbage (15.4 aphids on the 17th day). The maximum age-specific net aphid killing rates (w_x) of *A. asychis* feeding on the aphids on chili pepper and cabbage were 24.8 aphids per female on the 15th day and 15.4 aphids per female on
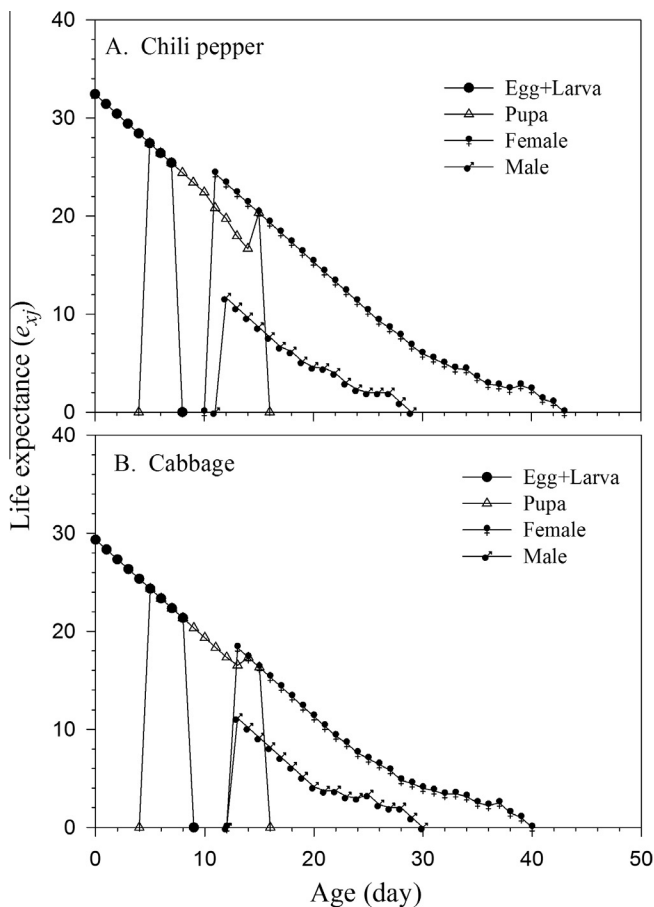

Fig. 3. Life expectancies (e_{xj}) of *Aphelinus asychis* parasitizing and feeding on *Myzus persicae* on chili pepper (A) and cabbage (B).
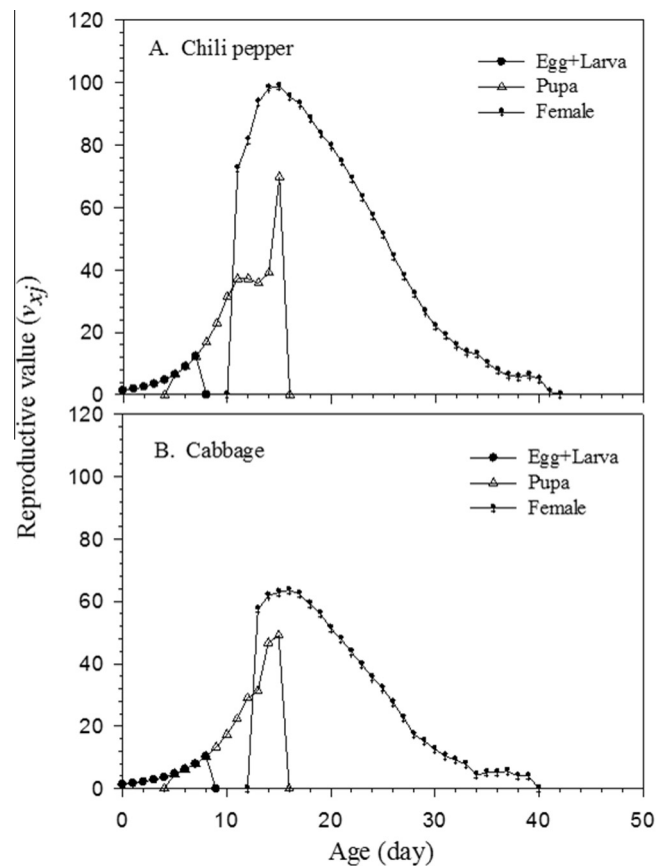

Fig. 4. Reproductive values (v_{xj}) of *Aphelinus asychis* parasitizing and feeding on *Myzus persicae* on chili pepper (A) and cabbage (B).
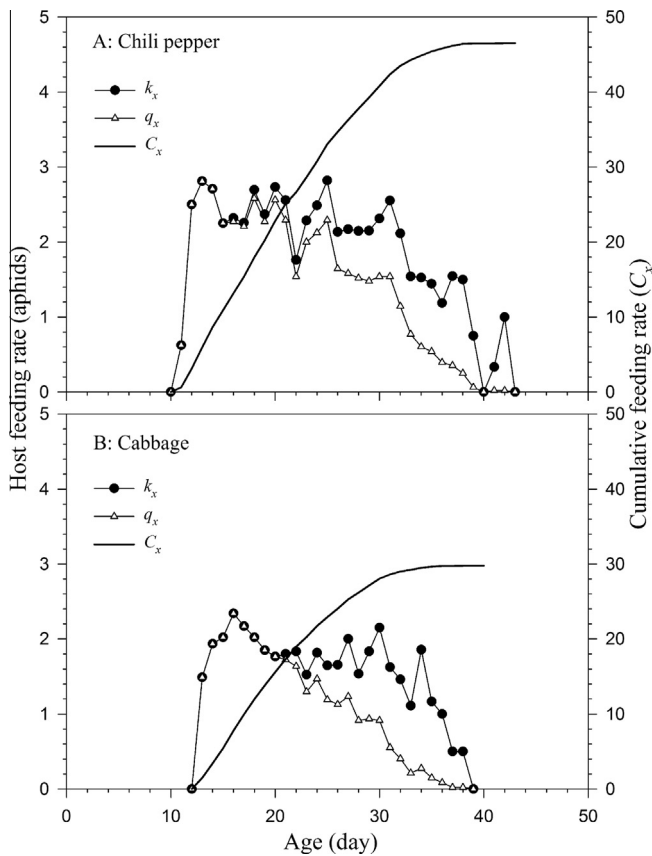
Fig. 5. Age-specific feeding rates (k_x), age-specific net feeding rates (q_x) and cumulative feeding rates (C_x) of *Aphelinus asychis* parasitizing and feeding on *Myzus persicae* on chili pepper (A) and cabbage (B), with the age being counted from birth.

Fig. 6. Age-specific non-effective parasitism rates (g_x), age-specific net non-effective parasitism rates (h_x) and cumulative non-effective parasitism rates (N_x) of *Aphelinus asychis* parasitizing and feeding on *Myzus persicae* on chili pepper (A) and cabbage (B), with the age being counted from birth.

the 17th day, respectively, and the former was greater than the latter. The net aphid killing rate (Z_0) of *A. asychis* on chili pepper was 384.1 aphids per individual, which is significantly greater than the 198.8 aphids on cabbage.

The stable aphid killing rate and finite aphid killing rate are listed in Table 2. The stable aphid killing rate and finite aphid killing rate of *A. asychis* feeding on the aphids on chili pepper were 0.4594 and 0.6286, respectively, which were both significantly greater than the corresponding values on cabbage. The transformation rate (Q_p) is also listed in Table 2. The Q_p value of *A. asychis* reared on the aphids on chili pepper was 1.2355 aphids for the production of each egg, while 1.3054 aphids were needed for *A. asychis* reared on aphids on cabbage.

4. Discussion

In this study, we found that the developmental duration of *A. asychis* preying on *M. persicae* nymphs on cabbage was longer than on chili pepper, which suggested that the host plant does affect the developmental duration of parasitoids. It was already known that host species, age and size affect the host suitability of parasitoids, especially the developmental duration (Smilowitz and Iwantsch, 1973; Hu et al., 2002). Raney et al. (1971) suggested that the immature development of *A. asychis* fed on *Schizaphis graminum* (Rondani) was faster than when reared on *Rhopalosiphum maidis* (Fitch) or *Sipha flava* (Forbes). Starý (1988) suggested that the developmental duration of aphelinid parasitoids is partially influenced by the host species. Lee and Elliott (1998) reported that the total developmental duration of the Chinese *A. asychis* strain with third instar nymphs of the Russian wheat aphid as host was longer than for the Moroccan *A. asychis* strain. Bernal and
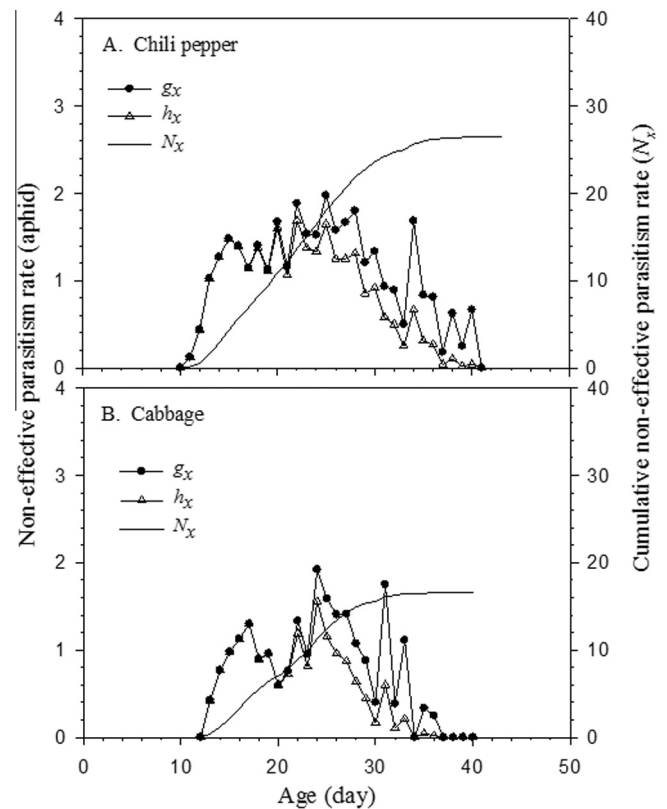
Gonzalez (1993) showed the variable developmental duration of *A. asychis* fed on *D. noxia*.

We found that the pupal mortality of *A. asychis* in *M. persicae* nymphs on chili pepper (4%) was less than on cabbage (6%), which suggested that the pupal mortality of *A. asychis* might be influenced by the host plant. Earlier studies showed that the pupal mortality could be affected by many factors, especially the host species and developmental stage (Raney et al., 1971; Tatsumi and Takada, 2005).

Our data showed that the percentage of *A. asychis* female adults was 72% on chili pepper and 68% on cabbage. Previous studies showed that proportions of female *A. asychis* adults might vary with host species (Jackson and Eikenbary, 1971; Raney et al., 1971). Cate et al. (1977) observed that a high percentage of female parasitoids (95.0%) emerged from older *S. graminum*, while only 54.7–56.0% females emerged on young and intermediate aged aphids. Moreover, temperature may also affect sex ratio. Bernal and Gonzalez (1993) found the highest proportion of females (70%) on *D. rapae* at 7.2 °C and the lowest (50%) at 29.4 °C.

We found that the host species had a prolonged effect on the female longevity, and the female adult longevity on cabbage was 5.3 days shorter than on chili pepper (17.8 days vs. 23.1 days). The differences might be caused by the nutrition of the host aphids feeding on different host plants (Raney et al., 1971; Jackson and Eikenbary, 1971). Previous studies showed, however, that the host instar had some effects on female longevity. Sengonca et al. (2008) reported that the longevity of *A. asychis* females parasitizing and host-feeding on 1–2 day old cotton aphid nymphs was much longer (32.8 days) than for *A. asychis* feeding on 4–5 day old nymphs (25.2 days) and adults (24.2 days). Byeon et al. (2011a) found that the longevity of *A. asychis* female adults with second and third instar *A. gossypii* as the host was 21.3 d for females.
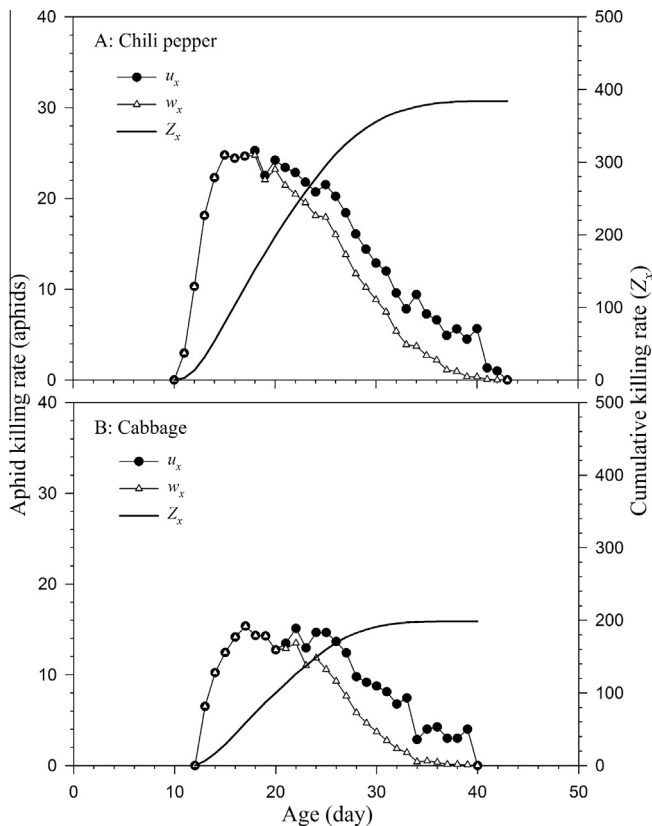
Fig. 7. Age-specific aphid killing rates (u_x), age-specific net killing rates (w_x) and cumulative killing rates (Z_x) of *Aphelinus asychis* parasitizing and feeding on *Myzus persicae* on chili pepper (A) and cabbage (B), with the age being counted from birth.

Because more aphids were supplied than the parasitoids could parasitize and feed, superparasitism was not observed in this study. This result is consistent with earlier reports on *Aphelinus* species (Mackauer, 1982; Wahab, 1985; Bai and Mackauer, 1990b).

In this study, we distinguished nutritional feeding, effective parasitism, non-effective parasitism. In this way, we can weigh the relative importance of these three factors. When feeding on the aphids on cabbage and chili pepper, the curves of the age-stage specific fecundities (f_{x3}) of *A. asychis* reached peaks in reproduction, respectively, and the values of f_{x3} were 16.7 offspring at age 17 d and 29.1 offspring at age 15 d, respectively. These results were different from previously reported findings (Mackauer, 1982; Sengonca et al., 2008; Byeon et al., 2011a,b). In our study, the maximum daily fecundity of *A. asychis* with second instar *M. persicae* as the host on chili pepper was 29.1 eggs/day, which was greater than 14.8 eggs/day with 1–2 day old *A. gossypii* nymphs, as reported by Sengonca et al. (2008), and less than 24.8 eggs/day with second instar nymphs of *A. gossypii* by Byeon et al. (2011a). The total fecundity (414.6 eggs/female) of *A. asychis* with second instar *M. persicae* on chili pepper as the host was almost twice as many as with 1–2 day old *A. gossypii* nymphs (232.3 eggs/female) (Sengonca et al., 2008) and much more than with second instar nymphs of *A. gossypii* (342.9 eggs/female) (Byeon et al., 2011a). These differences might be due to different host species and host plants. These results may also indicate that *A. asychis* is a better biological control agent for controlling *M. persicae* infesting chili pepper than *A. gossypii* infesting cotton and cucumber.

To produce more progeny, adult *A. asychis* females need to prey on hosts to obtain nutrition. Therefore, the feeding rate on aphids infesting different plants should be counted. Tatsumi and Takada (2005) found that the number of *A. gossypii* killed by predation was significantly greater than for *M. persicae* or *M. euphorbiae*.

Sengonca et al. (2008) also found that *A. asychis* could feed on up to 161.2 1–2 day old *A. gossypii* nymphs, 87.9 4–5 day old nymphs, and 42.7 aphid adults reared on cucumber (*Cucumis sativus* L.). These studies showed that host species and instars had significantly different influences on the host-feeding. Moreover, the difference in the host-feeding number between Sengonca et al. (2008) and Byeon et al. (2009) might be due to geographical location and test operation. In this study, we found that the parasitoids fed on more aphid nymphs on chili pepper than on cabbage, indicating that the host-feeding of the parasitoids was affected by the host plant and aphid species.

Previous studies showed that the developmental stage of aphids could affect host-feeding and parasitism by *A. asychis* female adults (Sengonca et al., 2008) and that host nymphal stages can affect the population dynamic variation of both the aphids and the parasitoids, ultimately affecting the success of biological control by parasitoids (Pak, 1986; Hagvar and Hofsvang, 1991). There will be an advantage if the parasitoids can parasitize and prey earlier instars, which will reduce crop damage and the number of individuals that develop to adulthood (Tsai and Wang, 2002). The preference for younger aphid stages has been previously described for other *Aphelinus* species (Cate et al., 1977; Gerling et al., 1990; Kouame and Mackauer, 1991; Tang and Yokomi, 1996). Furthermore, the preference of *Aphelinids* for younger host instars has been speculated to be associated with aphid defense reactions, as the older and larger aphids are stronger, making parasitization more difficult than on younger or smaller aphids (Wilbert, 1964; Gerling et al., 1990; Tang and Yokomi, 1996). Gerling et al. (1990) described the instar-specific defense of pea aphid (*Acyrthosiphon pisum* Harris) nymphs and deemed that oviposition success is probably influenced by aphid behavior such as instar-specific escape and defense reactions. Sengonca et al. (2008) found that the fecundity and host-feeding of *A. asychis* female adults with 1–2 day old *M. persicae* nymphs as the host were higher than with 4–5 day old nymphs and adults. In addition to mechanical defense reactions, there are most likely internal host defense reactions, such as cellular or humoral reactions. We found that the fecundity and host-feeding of *A. asychis* female adults reared on second instar nymphs of *M. persicae* on chili pepper was greater than for *A. asychis* female adults fed on aphids on cabbage, which indicates that the host-feeding and parasitism abilities of *A. asychis* female adults might be affected by defense reactions from both the aphids and the host plant.

Our study also indicated that the shorter developmental duration and higher proportion of females make *A. asychis* a better natural enemy for the biological control of *M. persicae* on chili pepper than on cabbage. However, for a comprehensive evaluation of the total control efficiency of *A. asychis* on *M. persicae* infesting chili pepper and cabbage, daily host-feeding and parasitism number of aphids (both effective parasitism and non-effective parasitism) were incorporated as the aphid killing rate (Z_0). Furthermore, we combined the net killing rate (Z_0) with the finite rate (λ) and the stable age-stage distribution to compare the effect of *A. asychis* on controlling *M. persicae*. In our research, the finite killing rate (ϑ) on chili pepper was significantly greater than on cabbage, indicating that the cumulative control efficiency of *A. asychis* on *M. persicae* infesting chili pepper will be better than on cabbage.

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