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Life History Parameters and Temperature Requirements for Development of an Aphid Parasitoid *Aphelinus asychis* (Hymenoptera: Aphelinidae)

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ABSTRACT We assessed the life history parameters and temperature requirement of a Korean population of the endoparasitoid *Aphelinus asychis* Walker (Hymenoptera: Aphelinidae), using *Aphis gossypii* Glover (Hemiptera: Aphididae) as a host.

We first measured the time from egg to mummification (i.e., pupation) and mummification to adult emergence (i.e., pupal period) at 25°C. The pupal period was significantly longer than the egg to pupation period in both genders, unlike in other regional populations of the species. Females produced an average of 342.9 mummies, the highest reported fecundity among the various regional populations of this species. Age-specific realized fecundity peaked between the 4-7th day (23.3-24.8 mummies a day). The intrinsic rate of increase (r_m) was 0.255 offspring per female per day.

The parasitoids were then reared at eight constant temperatures between 15 and 32.5°C. The developmental time from egg to adult emergence decreased from 27.8 to 9.8 d. The lower developmental thresholds (T_0), estimated by linear regression, for the egg to mummy, mummy to adult, and egg to adult stages were 6.7, 6.8 and 6.7, respectively. The thermal constants for each of the three periods were 115, 126, and 243 degree-days. We compared these parameters with published data of *A. asychis* from other regions reared on different hosts and representative species of aphid parasitoids in Aphidiinae (Braconidae) reared on hosts including *A. gossypii*. The T_0's of *A. asychis* were higher than those of *Aphidius colemani* and *Aphidius matricariae* when using *A. gossypii*.

KEY WORDS

cotton aphid, fecundity, temperature requirement, lower developmental threshold, thermal constant

Temperature plays a major role in the ecology and population dynamics of insect pests and their natural enemies (Andrewartha and Birch 1954, Kontodimas et al. 2004). The relationship between temperature and developmental rates in insects is generally linear over the range of temperatures to which they are exposed. Conversely, development rate becomes nonlinear at extreme, sublethal temperatures (Wagner et al. 1984).

The lower developmental threshold is the temperature below which no development occurs, and the thermal constant is defined as the amount of heat required to complete development from egg to adult emergence of insects (Andrewartha and Birch 1954). These two parameters are important for the purposes of biological control as they aid in selection of natural enemies that are best adapted to environments favoring target pests and for predicting seasonal abundance on a physiological time-scale (Wagner et al. 1991, Jervis et al. 2005).

The cotton aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae), is a polyphagous, cosmopolitan insect pest that has high reproductive potential (van Steenis and El-Khawass 1995) and infests cucurbitaceous crops including cucumber, watermelon and pumpkin as well as solanaceous crops including eggplant and tomato and malvaceous crops (cotton) (Kersting et al. 1999, Parrella et al. 1999). This aphid feeds on plant sap on underside of leaves and shoots, and can transmit viruses that result in reduced fruit yield (Hussein and Samad 1993). Aphid honeydew also promotes the growth of sooty mold fungus on the crop (Wood et al. 1988, Vasquez et al. 2006). Insecticides have been used extensively for control of *A. gossypii* but resistance to insecticides has been frequently observed **(**Kerns and Gaylor 1992, Wang et al. 2001). Given this, there have been a number of attempts to control *A. gossypii* using aphidiine parasitoids such as *Aphidius colemani* Viereck and *Aphidius matricariae* (Haliday) (Hymenoptera: Braconidae) **(**Bennison 1992, Bennison and Corless 1993, Goh et al. 2001, Nagasaka et al. 2005, Vasquez et al. 2006**)**. However, control by these aphidiine parasitoids was not always successful in the greenhouses because of the impact of hyperparasitoids (Nagasaka et al. 2005), as well as the occurrence of non-preferred aphid hosts (i.e., *Macrosiphum euphorbiae* Thomas and *Aulacorthum solani* Kaltenbach (Hemiptera: Aphididae)) (Nagasaka et al. 2005, Tatsumi and Takada 2005, Van Driesche et al. 2008). Therefore, studies on additional biological control agents of the aphids are required, which could enhance success in control of aphids under various greenhouse conditions.

Aphelinus asychis Walker (Hymenoptera: Aphelinidae) is a polyphagous endoparasitoid that is native to Europe, Asia, and Africa. This species is capable of parasitizing and host-feeding on as many as 40 aphid species including *A. gossypii* (Bai and Mackauer 1990, Li et al. 2007). This parasitoid has been considered as a potential candidate for the biological control of four aphid species commonly found in greenhouses: *A. gossypii*, *Myzus persicae* Sulzer, *A. solani* and *M. euphorbiae* (Hemiptera: Aphididae) (Takada 2002).

Understanding the biological characteristics, such as development, reproduction and survival of a parasitoid species is essential for pre-evaluation of its effectiveness as a biological control agent. However, there have been few integrated studies on these parameters for *A. asychis* in East Asian countries. Thus, our objective was to characterize the developmental time of the immature stages, age-specific fecundity, and survival of *A. asychis*. We also compare these life history parameters with other regional strains of *A. asychis* and other *Aphelinus* species, some of which are closely related to *A. asychis* (Zhu and Fang 2009). Furthermore, the effect of temperature on the development of East Asian *A. asychis* population is not fully explored. Therefore, we investigated the temperature requirements (developmental threshold and thermal constant) and optimal temperature range (in terms of low pupal mortality and high proportions of females) of *A. asychis*. We compared these parameters with published data from other regional strains of the parasitoid and another taxonomic group of aphid parasitoid, Aphidiinae.

Materials and methods

Insect Culture

We obtained parasitoids (*A. asychis*) from the black mummies of *Myzus persicae* found on Chinese cabbage, *Brassica campestris* L., in Hoengseong, the northern part of South Korea and identified as *A. asychis* (Li et al. 2007). Stock cultures of this parasitoid were maintained on green bug, *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae), cultured on barley, *Hordeum vulgare* L. var. *chalbori* because parasitoid rearing cost by using barley and *S. graminum* is lower than by using cucumber and *A. gossypii*. All insects were reared under a 16L:8D photoperiod in air-conditioned insectaries at 24−27°C and 50−70% RH.

Development Times of Immature Stages

We used cucumber (*Cucumis sativus* L. var. *baekchimdadagi*) seedlings at the three-to-five leaf stage and about 20 cm in height, cultured in planting media (Baroker, Seoul Bio Co., South Korea) in 8 cm diameter pots, in a growth chamber set at 25°C and 16L:8D. Adults of *A. gossypii* were allowed to produce nymphs on the cucumber seedlings for 12 h and the nymphs were allowed to develop for 2-3 d to prepare the second and third instar *A. gossypii* in the air-conditioned insectaries.

Mummies were placed in size 0 gelatin capsules (Bioquip, USA). After 24 h, we determined the gender of the emergent parasitoid adults. One female and two male parasitoids were then placed in a plastic tube (26 × 67 mm) for 4 h to facilitate mating. Following mating, 50 of the mated female wasps were placed into acrylic cages (27 × 27 × 27 cm) that contained cucumber seedlings infested with 150–350 second and third instar *A. gossypii*. The female wasps were allowed to oviposit for 8 h. The parasitoids were then removed and the cucumber seedlings infested with *A. gossypii* were transferred to growth chambers and cultured at 25^{o}C and 16L:8D. We checked the aphids every 12 h for mummy formation, following the removal of the female parasitoids for parasitization. Each mummy was carefully collected using a fine hair brush and transferred individually to size 0 gelatin capsules. The capsules were held in the growth chamber until emergence of the parasitoids. We recorded the times of mummification (i.e., pupation) and adult emergence to derive the development time from egg (introduction of female parasitoids) to mummification, mummification to adult and egg to adult emergence (the sum of the former two measures).

Age-specific Fecundity and Survival

We estimated age-specific fecundity and survival of *A. asychis* using a cohort of 12 *A. asychis* females that were reared from *S. graminum*. Parasitoid mummies were placed individually in size 0 gelatin capsules. We checked adult emergence every 12 h and determined the gender of each emerging individual. Each female was then caged with two males for 4 h, after which one male was removed and the remaining male and the female were transferred together into an experimental arena containing 7 cm cucumber leaf disks infested with 50 2–2.5 day old nymphs, corresponding to the second instars, which were prepared as follows: Adults of *A. gossypii* were allowed to produce nymphs on cucumber seedlings for 12 h. Then, 50 nymphs were inoculated on a cucumber leaf disk placed ventral-side-up on water-saturated cotton in a Petri dish (9.3 × 4 cm) and allowed to develop for 2 d. A round piece of gauze (4 cm diameter) was placed over a hole on the lid for ventilation. The Petri dishes were replaced every 24 h with a fresh dish containing a leaf disk with 50 *A. gossypii* until both the female and male parasitoids died. Each dish was held in an incubator at 25°C and 16L:8D until the aphids were mummified. The number of surviving adult parasitoids and the number of aphid mummies were recorded every 24 h.

The values of net reproductive rate (R_0), mean generation time (T) and intrinsic rate of natural increase (r_m) were obtained with the following equation given by Birch (1948).

$$R_0 = \sum l_x m_x$$

$$T = \sum x l_x m_x / R_0$$

$$\sum l_x m_x \exp(-r_m x) = 1$$

where x is the female age (starting from 0 d-old egg), l_x is the proportion of females surviving to the age, m_x is the expected number of daughters produced per female alive at the age x, and T is the generation time.

Effect of Temperature on Development, Gender, and Pupal Mortality

We prepared *A. gossypii* that were parasitized by *A. asychis* females on cucumbers in a growth chamber at 25 °C and 16L: 8D as described earlier. After oviposition, the parasitoids were removed and each plant was transferred into growth chambers adjusted to one of eight temperatures: 15, 17.5, 20, 22.5, 25, 27.5, 30, or 32.5°C, and 16L:8D. The temperatures in the chambers were measured by HOBO Data Loggers (Onset Computer

Corp., USA). Following the removal of the female parasitoids for parasitization, we observed the aphids twice each day (at 12 h intervals, starting from the time we introduced female parasitoids for oviposition) for mummy formation. Each mummy was carefully collected by using a fine hair brush and transferred individually to size 0 gelatin capsules. The capsules were held in the growth chambers at one of the eight temperatures and were checked twice a day for adult emergence. We recorded the gender of emerging parasitoid adults and the number of dead pupae. Pupae were considered dead if no parasitoid emerged from them for a week after emergence of parasitoids from the pupal population ceased. The possibility cannot be excluded that the 8 h parasitization period and subsequent transfer to cooler temperatures may have caused underestimation of development times at the lower temperatures.

Statistical Analysis

Developmental rate models. We investigated the effect of temperature on the developmental rate of three stages (i.e., egg to mummy, mummy to adult and egg to adult emergence) using linear regression. We used the model: $Y = bX + a$, where Y is developmental rate (1/(number of days required for development)); X is the temperature, a and b are the intercept and slope parameters obtained from the linear regression. The lower developmental threshold temperature (T_0) is the intercept of the temperature axis of the regression (i.e., $T_0 = -a/b$) and the thermal constant (degree-days, DD) is the reciprocal of the regression coefficient (i.e., thermal constant = $1/b$) (Campbell et al. 1974). Data points that induced nonlinearity in development-temperature relation (i.e., 15°C and 32.5°C) were discarded in the linear regression. SE's of T_0 and DD were estimated following Campbell et al. (1974).

Comparison with other aphid parasitoids. We analyzed the data for the egg-to-adult T_0 and *DD* of *A. asychis* and aphidiine parasitoids (*A. matricariae*, *A. colemani*, and *Diaeretiella rapae* (McIntosh)) from published works. To ensure the thermal data were comparable to our study, we re-estimated the T_0 and *DD* from the published studies by linear regression on mean temperatures, discarding data point(s) that would induce nonlinearity.

Life history parameters. We compared the development times for egg to mummification, mummification to adult emergence and egg to adult emergence between genders using unpaired *t* tests. The time periods from egg to mummification and from mummification to adult emergence within each gender were also compared using unpaired *t* tests. Relations between temperature and proportion of females or pupal mortality were analyzed using generalized linear models with logit link and binomial error family. Individuals died before reaching adult stage were discarded from the development time data.

Data on developmental times of the two genders were pooled for linear regression. We used Welch's test to analyze the effect of temperature on development of *A. asychis* because the test for homogeneity of variance for the development data deviated significantly among temperatures (Bartlett's test, $F = 19.24$; $df = 7$; $P < 0.0001$ for egg to mummy, $F = 21.48$; $df = 7$; $P < 0.0001$ for mummy to adult emergence, $F = 8.58$; $df = 7$; $P < 0.0001$ for egg to adult emergence) after one-way ANOVA. We compared the lower temperature threshold and thermal constant between *A. asychis* and aphidiines using a nonparametric Wilcoxon-Mann-Whitney test (Wilcoxon 1945, Mann and Whitney 1947).

JMP 8.0 (SAS Publishing 2008) was used to perform all the statistical tests.

Results

Development Times of Immature Stages

The development times from egg to mummy, mummy to adult emergence, and egg to adult emergence at 25°C were 6.0, 7.9 and 13.9 d, respectively, for females and 5.9, 7.4 and 13.2 d for males (Table 1). The duration of development for the three immature periods were all significantly shorter in males than in females (for egg to mummification, $t = -3.47$, $df = 260$, $P < 0.001$; for mummification to adult emergence; $t = -6.36$, $df = 260$, $P < 0.001$; for egg to adult emergence, $t = -6.66$, $df = 260$, $P < 0.001$). The developmental time from mummification to adult emergence was significantly longer than that from egg to mummification in both genders (female: $t = 31.5$, $df = 270$, $P < 0.001$; male: $t = 25.5$, $df = 250$, $P < 0.001$).

Age-specific Fecundity and Survival

When *A. asychis* encountered the host aphid *A. gossypii*, it touched *A. gossypii* with its antennae before inserting its ovipositor for host-feeding and ovipositing. Males and mated females survived 8.2 and 21.3 d, respectively at 25°C (Table 2, Fig. 1). On average, the female laid eggs that produced 14.9 mummies a day and a total of 342.6 mummies during her life span (Table 2). The fecundity of *A. asychis* was higher than in *A. asychis* from other locations (Appendix 1).

Daily fecundity peaked (23.3–24.8 mummies a day) between the 4–7th day and increased and decreased repeatedly during the first 12 days, but declined gradually thereafter (Fig. 1). The daily fecundity curve is approximated by a typical triangular curve (Roff 1992, Kindlmann et al. 2001) in which mummy production first increased and then slowly decreased (Fig. 1).

Based on these data, the r_m of *A. asychis* at 25°C was 0.255 d^{-1}. The T and R_0 were 23.03 d and 145.1 female progenies, respectively.

Effect of Temperature on Development, Gender, and Pupal Mortality

The development times for each of the three immature periods of *A. asychis* were significantly different among the eight different rearing temperatures ($F_{7,\,472.9} = 5397.7$; $P < 0.0001$ for egg to mummy, $F_{7,\,471.9} = 5925.4$; $P < 0.0001$ for mummy to adult emergence, $F_{7,\,482.4} = 7092.8$; $P < 0.0001$ for egg to adult emergence) (Table 3). The developmental time from egg to mummy decreased from 13.4 (at 15°C) to 4.9 d (at 32.5°C) as temperature increased. Likewise, the development time from mummy to adult emergence decreased from 14.3 to 4.8 d, and total time for immature development decreased from 27.8 to 9.8 d, as temperature increased from 15 to 32.5°C. The proportion of females and pupal mortality was not affected linearly by temperature (proportion of females, $\chi^2 = 0.0512$, $df = 1$, $P = 0.82$; pupal mortality, $\chi^2 = 0.0026$, $df = 1$, $P = 0.96$).

Developmental Rate Models

The rate of development of *A. asychis* from egg to mummy, mummy to adult emergence and egg to adult emergence increased linearly with temperature within the temperature range of 17.5−30°C. The linear regression equations for developmental rate in relation to temperature for the three immature periods were estimated as in Table 3. Based on these equations, the lower developmental threshold temperatures and the thermal constants were estimated for the three developmental periods (Table 4).

Comparison with Other Geographic Populations and Family

The estimated lower developmental threshold (T_0) of *A. asychis* was significantly higher than those of the two aphidiine species, *A. colemani and A. matricariae* when reared on *A. gossypii* (i.e., 1.96 SEs or 95% confidence intervals did not overlap). The T_0's were also higher in seven geographical populations (or nine parasitoid-host population combinations) of *A. asychis* than in aphidiine parasitoid species ($U_{6,9} = 50.0$, $P < 0.005$, Appendix 2). We found no difference in the thermal constants (*DD*) between *A. asychis* and aphidiine parasitoids ($U_{6,9} = 27.5$, $P > 0.9$, Appendix 2).

Discussion

The pupal (i.e., mummy) period of both genders of the Korean population was longer than the egg to pupa period (Table 1). Furthermore, the pupal period of the Korean population (7.9 d in females and 7.4 d in males) was longer than that of the Kyoto population (6.6 d in females and 6.3 d in males, reared on 4-5 d old host), whereas the egg to mummy period was shorter in the former than the latter populations (Sengonca et al. 2008). These differences among the strains might be attributed partly to adaptation to local climates and/or attack by hyperparasitoids. Lee and Elliott (1998) demonstrated that *A. asychis* that is reared in a warmer climate has shorter developmental time in the pupal stage (3.7 d at 26°C) than a strain reared in a cooler climate (6.4 d at 26°C). The authors suggested that this is because the parasitoid is exposed to extreme high temperatures during the exposed, sessile pupal stage in the warmer climate. Desiccation may also be a critical factor for survival in this environment. In addition, pupal hyperparasitoids may play a role in shortening pupal period (Lee and Elliott 1998). Such evolution in the length of host vulnerable stage is observed in a laboratory host-parasitoid system (Pimentel et al. 1978). As a consequence of the shorter duration of vulnerability, host-parasitoid systems are more likely to persist (Tuda and Shimada 1995, 2005, Tuda 1996).

The fecundity of *A. asychis* in the present study was higher than in *A. asychis* from other locations with different host aphids (Appendix 1). The high level of fecundity that we observed might be a function of host availability. In our study there was an abundant supply of aphids that were suitable for both host-feeding and parasitization (see also Force and Messenger 1964a in Appendix 1). Furthermore, the number of mummies formed might vary across the distribution range of the parasitoids (Bernal and Gonzalez 1993). For example, Elliott et al. (1999) reported differences in mummy formation and survival rates in *A. asychis* from different regions (high in strains from Kazakhstan and China and low in a Moroccan strain). In addition, the body size of females, a proximate factor contributing to fecundity, is affected directly by the size (age) and suitability of hosts (see Sengonca et al. 2008 for *A. asychis*). Both the reared and experimental aphid species used in the present study are probably equally suitable as hosts, as was observed in the other East Asian population of *A. asychis* (Elliott et al. 1999) and might also explain, in part, the high fecundity we observed.

We speculate that the repeated increase and decrease in the daily fecundity is associated with host-feeding and subsequent oogenesis in a synovigenic parasitoid such as *A. asychis* (cf., Wu and Heimpel 2007). Daily fecundity increased most dramatically from

6 to 21 during the first two days of the adult period. This corresponds with observations of the number of eggs in *A. albipodus* (Wu and Heimpel 2007), a potential sibling species of *A. asychis* (Zhu and Fang 2009).

We observed high fecundity and longevity of the South Korean *A. asychis*. These parasitoids also caused high mortality in *A. gossypii* by non-reproductive host killing (Byeon et al. 2009) as does the other East Asian population (Tatsumi and Takada 2005, Sengonca et al. 2008). *A. asychis* has high ability for host searching (in comparison with *A. colemani*, Byeon et al. 2011), a trait that is characteristic of aphelinid wasps in general (Viggiani 1984). Bernal and Gonzalez (1993) demonstrated that pupal mortality was lower in *A. asychis* (44 and 65% for different geographic strains at 29.4°C) than in aphidiine wasps, *A. matricariae* (100%) and *D. rapae* (92%) at the same high temperature. They suggest that *A. asychis* is better adapted to regions of higher temperature than aphidiine parasitoid species. Pupal mortality of South Korean *A. asychis* range between 11.1–18.1% at 27.5–32.5 °C (Table 3) and this not only supports their suggestion but also indicate the Korean population is even more adapted to high temperature than are conspecific populations from Chile and France. Together, these observations suggest that the South Korean strain of *A. asychis* has considerable potential as a biological control agent of *A. gossypii*, supporting the consideration of aphelinids as important control agents of aphids in greenhouses (van Lenteren et al. 1997).

Temperature did not have a linear effect on the sex ratio of the offspring. However, optimal temperature for the production of the highest proportion of females was 22.5°C if the datum at 32.5°C was excluded (see later). Schlinger and Hall (1959) noted that the proportion of *Aphelinus semiflavus* (a junior synonym of *A. aphelinus*) females decreased as temperature increased (from 95–98% at 18.3–22.2°C to $\leq$ 1% at 25.6–29.4°C).

Conversely, the proportion of females was highest at intermediate temperatures (64–65% at 18–27°C) in *Aphelinus gossypii* (Tang and Yokomi 1995). Likewise, there was no linear relation between temperature and sex ratio in *Aphelinus spiraecolae*, and the proportion of females was highest at the two extreme temperatures, 15°C (70.8%) and 30°C (69.3%). In our study, proportion of females at 32.5°C was higher than other temperatures and the size of dead mummies was very small (Y. W. B., pers. observ.). Aphelinid wasps are known to allocate male progeny to small hosts, as do other hymenopteran insects. Given this, it is likely that the mortality is gender-biased towards males at the highest temperature.

The response of parasitoid to ambient temperature is one of many attributes, including fecundity, search efficiency, and host preference that, acting in concert with environmental factors, will determine the outcome of attempts at biological control of a host (Bernal and Gonzalez 1993). Besides climate, host aphids may also affect the thermal requirements of the parasitoid (Raney et al. 1971). Therefore, integration of available knowledge on environment and species combination to target will be required for each specific case of biological control.

Given that parasitoids have difficulty in colonizing an area when hosts have not reached a developmental stage suitable for parasitization, the success of biological control efforts might depend on the use of natural enemies that emerge after host development (Campbell et al. 1974). The onset of seasonal emergence of parasitoids might be estimated using the lower developmental threshold. Thus, parasitoids with a higher developmental threshold than their hosts are expected to appear later than their hosts (Bernal and Gonzalez 1993). The developmental threshold of *A. asychis* (6.7°C) estimated in the present study was higher than that of its host, *A. gossypii* (5.0°C, Kim et al. 2004). However, other ecological factors such as diapause (Tatsumi and Takada 2006), foraging behavior (Li et al. 1992, De Farias and Hopper 1999), searching efficiency, functional response (Bai and Mackauer 1990, Byeon et al. 2011), and host preference, as well as evolutionary potential of these traits (c.f., Tuda and Bonsall 1999, Hufbauer and Roderick 2005) must be considered prior to using this parasitoid in biological control program.

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Table 1. Development times (d) of the females and males of *A. asychis* on *A. gossypii* at 25°C.

Stage	Female		Male	
	Mean ± SE	Range	Mean ± SE	Range
Egg to mummification	6.0 ± 0.3	6.0-7.0	5.9 ± 0.3	5.5-6.5
Mummification to adult emergence	7.9 ± 0.6	7.0-8.5	7.4 ± 0.6	6.0-9.0
Egg to adult emergence	13.9 ± 0.3	12.5-13.5	13.2 ± 0.8	12.0-15.0
n	136		126	

Table 2. Longevity (d) and fecundity (number of mummies formed) of *A. asychis* on *A. gossypii* at 25°C ($n = 12$)

	Mean ± SE	Range
Longevity in females	21.3 ± 0.9	14-24
in males	8.2 ± 0.5	6-11
Fecundity per day	14.9 ± 0.4	13-17
Fecundity until parasitoid died	342.6 ± 13.2	237-404

Table 3. Development times from egg to mummy, mummy to adult emergence and egg to adult emergence of *A. asychis* at eight constant temperatures (days, means ± SE). Means within the same period were significantly different among different temperatures for all three periods (see text). *n* refers to the number of emerging adults

Temp. (°C)	*n*	Period			Prop. of females	Pupal mortality (%)
		Egg to mummy	Mummy to adult emergence	Egg to adult emergence		
15.0	97	13.4 ± 0.05	14.3 ± 0.05	27.8 ± 0.09	0.474	13.4
17.5	119	11.5 ± 0.05	10.3 ± 0.05	21.7 ± 0.05	0.471	16.8
20.0	173	9.1 ± 0.04	9.6 ± 0.04	18.7 ± 0.07	0.509	9.9
22.5	255	7.2 ± 0.03	8.0 ± 0.03	15.2 ± 0.04	0.584	16.4
25.0	262	6.0 ± 0.03	7.6 ± 0.03	13.5 ± 0.05	0.519	18.4
27.5	97	5.6 ± 0.05	6.5 ± 0.05	12.1 ± 0.09	0.526	15.6
30.0	232	5.2 ± 0.03	5.1 ± 0.03	10.3 ± 0.06	0.517	11.1
32.5	138	4.9 ± 0.04	4.8 ± 0.04	9.8 ± 0.08	0.652	18.1

Table 4. Linear regression equations of developmental rate in relation to temperatures, estimated lower developmental threshold (T_0) and thermal constant (*DD*) for the immature stages of *A. asychis*. Data on development of egg to mummy, mummy to adult emergence and egg to adult emergence were obtained at six constant temperatures between 17.5 and 30°C

Period	Slope, *b* (± SE)	Intercept, *a* (± SE)	ANOVA parameters			R^2	T_0 (± SE) (°C)	*DD* (± SE) (°C d)
			F	*df*	*P*			
Egg – mummy	0.00867 (± 0.00012)	-0.0582 (± 0.003)	5433.6	1137	< 0.001	0.827	6.7 (± 0.25)	115 (± 1.6)
Mummy – adult emergence	0.00795 (± 0.000098)	-0.0543 (± 0.002)	6569.9	1137	< 0.001	0.853	6.8 (± 0.22)	126 (± 1.6)
Egg – adult emergence	0.00412 (± 0.000038)	-0.0278 (± 0.0009)	11595.6	1137	< 0.001	0.911	6.7 (± 0.16)	243 (± 2.2)

Appendix 1. Comparison of longevity of adult female, numbers of eggs deposited and aphids killed by non-reproductive activity among seven *Aphelinus* species

Aphelinus species	Temp. (°C)	Host aphid	Reared host	No. and age/stage of aphids provided	Longevity of female (d)	Number, time and remating chance with males	Male longevity (d)	Mean number of eggs deposited		Mean number of aphids killed		Total no. attacked aphids	References
								daily	total	daily	total		
asychis	26.7	*Schizaphis graminum*	*S. graminum*	20 (mixed stage)	23.4	1, -, yes	-	ca. 10*	233*	ca. 1.5	30.4	263.4	Cate et al. (1973)
asychis	25	*Acyrthosiphon pisum*	*A. pisum*	40 (2nd instar)	-	unknown, no	-	ca. 8	-	ca. 1	-	-	Bai and Mackauer (1990)
asychis	25	*Aphis gossypii*	*A. gossypii*	20-50 (1-2 d-old)	32.8	unknown, no	15***	7.3*	232.3*	7.5	161.2	393.5	Sengonca et al. (2008)
				20-50 (4-5d-old)	25.2			1.7*	21.1*	4.0	87.9	109	
				20-50 (adult)	24.2			0.7*	44.7*	3.8	42.7	87.4	
asychis	25	*A. gossypii*	*S. graminum*	50 (2nd instar)	21.3	2, 4h, yes	8.2	14.9*	342.6*	3.3**	73.9**	416.5	Present study
semiflavus	26.7	*Therioaphis maculata*	*T. maculata*	75-100 (mixed stage)	ca. 26	unknown	-	ca. 14.8	385	-	-	-	Force and Messenger (1964a)
abdominalis	20	*Sitobion avenae*	*S. avenae*	150 aphids / 5 d (mixed stage, large cage)	51	unmated	-	ca. 11	ca.574	-	-	-	Höller and Haardt (1993)
					52	1, -, yes	5	ca. 14.4	ca.751	-	-	-	
albipodus	26.7	*Diuraphis noxia*	*D. noxia*	100 (mixed 3rd & 4th instar and adult)	16.4	1, -, yes	10	17.9*	294.7*	-	-	-	Bernal et al. (1997)
albipodus	25	*Aphis glycines*	*A. glycines*	50 1st instar	-	1, 3h, no	-	ca. 22	-	ca. 5	-	-	Wu and Heimpel (2007)
				50 2nd instar				ca. 13		ca. 8			
				50 3rd instar				ca. 12		ca. 4			
				50 4th instar				ca. 4		ca. 2			
				50 adult alate				ca. 1		ca. 2			

flavus	-	*Drepanosiphum platanoidis*	*D. platanoidis*	6 (1st instar)	27	unmated	-	1.8	48	1.2	28	76	Hamilton (1973)
gossypii	18	*A. gossypii*	*A. gossypii*	30 (3rd instar)	8	2 or 3, -, no	-	8.0	57	1.5	10.7	67.7	Tokumaru and Takada (1996)
gossypii	25	*A. gossypii*	*A. gossypii*	50 (24-48 h old)	26.3	1, 6h, yes	1	22.8	599*	ca. 3-4	87.9	676.9	Perng and Liu (2002)
spiraecolae	24	*Aphis spiraecola*	*A. spiraecola*	50 (2nd & 3rd instar)	17.8	2, 4h, no	-	6.7	138.2	1.9	27.1	165.3	Tang and Yokomi (1996)

* Number of mummies formed.

** Byeon et al. (2009)

*** Estimated without female

Appendix 2. Comparison of lower development threshold temperatures (T_0) and thermal constants (*DD*) of *A. asychis* and aphidiine parasitoids of different geographic origins. Numbers in bold are the parameters for parasitoids when using *A. gossypii*

Parasitic wasps	Country of origin	Host aphids	T_0 (±SE,°C)	*DD* (±SE)	References
Aphelinus asychis (as *A. semiflavus*, female)	Middle East and Southern Europe	*Therioaphis maculata*	10.6±0.82	190±11.4	Re-estimated from Force and Messenger (1964b)
A. asychis	Iran	*Sipha flava*	6.2±1.53	301±20.6	Re-estimated from Raney et al. (1971)
		Schizaphis graminum	12.7±0.51	177±6.4	
		Rhopalosiphum maidis	11.6±2.93	199±34.2	
A. asychis	Chillan, Chile	*Diuraphis noxia*	7.5±0.81	238±15.5	Re-estimated from Bernal and Gonzalez (1993)
A. asychis	Antibes, France	*D. noxia*	8.0±1.23	233±23.5	
A. asychis	Pingluo, China	*D. noxia*	9.2±0.65	215±11.8	Re-estimated from Lee and Elliott (1998)
A. asychis	Sette, Morocco	*D. noxia*	10.5±0.64	181±10.9	
A. asychis	Hoengseong, Korea	*Aphis gossypii*	**6.7±0.16**	**243±2.2**	Present study
Aphidius matricariae	Northern Iraq	*D. noxia*	2.4±0.66	285±15.4	Re-estimated from Bernal and Gonzalez (1993)
Diaeretiella rapae	Northwestern Pakistan	*D. noxia*	4.6±0.68	242±11.0	
Aphidius colemani	Tehran, Iran	*A. gossypii*	**6.3±0.19**	**187±2.8**	Re-estimated from Zamani et al. (2007)
		Myzus persicae	6.7±0.59	181±8.8	
Aphidius matricariae	Tehran, Iran	*A. gossypii*	**6.2±1.28**	**212±26.4**	
		M. persicae	6.4±1.00	213±17.1	

Figure legend

Fig. 1. Daily fecundity and percentage survival of *A. asychis* adults when provided with 50 *A. gossypii* (second instar) per day at 25°C.