Life tables and development of *Amblyseius swirskii* (Acari: Phytoseiidae) at different temperatures

Heung-Su Lee · David R. Gillespie

Abstract Development time, reproduction, survival and sex ratio were determined for the omnivorous mite *Amblyseius swirskii* at nine constant temperatures (13, 15, 18, 20, 25, 30, 32, 34 and 36°C) on pepper leaf disks with cattail, *Typha latifolia*, pollen for food. These data were used to derive life table parameters at these constant temperatures. No development was observed at 13°C. The lower development threshold, based on the fit to the linear portion of the development curve, was 11.3°C. The upper development threshold was 37.4 ± 1.12°C, and the optimum temperature was calculated to be 31.5°C. Average lifetime fecundity ranged from a low of 1.3 ± 0.24 eggs/female at 15°C to a high of 16.1 ± 0.34 eggs/female at 25°C, and r_m was greatest at 32°C. Non-linear regression of the relationship between temperature and r_m produced an estimate of 15.49 ± 0.905°C for the lower threshold for population growth and 36.99 ± 0.816°C for the upper threshold for population growth, and an optimum temperature of 30.1°C. These values suggest that *A. swiskii* populations should grow quickly in response to food availability (pollen or prey) between 20 and 32°C, but that, especially below 20°C, population growth could be slow and impacts on prey populations should be monitored carefully.

Introduction

Most life-processes in poikilothermic arthropods such as insects and mites, are determined by the temperature of the surrounding environment (Trudgill et al. 2005). In poikilotherms,

H.-S. Lee
Division of Plant Environment, Gyeongnam Agricultural Research & Extension Services, Jinju 660-370, Korea
e-mail: Lhs2khk@paran.com

D. R. Gillespie (✉)
Agriculture and Agri-Food Canada, Pacific Agri-Food Research Centre, PO Box 1000, Agassiz, BC V0M 1A0, Canada
e-mail: Dave.Gillespie@agr.gc.ca

temperature affects fundamental population processes such as development rate, birth rate, death rate and generation time, and consequently, drives population growth (Campbell et al. 1974; Cloutier et al. 1995; Clarke 2003; Roy et al. 2002; Trudgill et al. 2005; Bensadia et al. 2006; Anton et al. 2007). Population growth is particularly important in biological control programs against pest arthropods where the population of biological control agents is anticipated to increase following an initial release. The available heat units in the environment following release will, in part, determine population growth, and can be an important factor affecting the success of a biological control agent (Stenseth 1979; Hulspas-Jordaan and van Lenteren 1989). Therefore, knowledge of the effects of temperature on the growth of populations of natural enemies can be important for determining, for example, release timing, release numbers, and geographic regions in which a particular natural enemy can be used. Several recent studies have assessed the population growth and biological control potential of natural enemies in relation to temperature (e.g., Lee and Ahn 2000; Roy et al. 2002; Kasap and Şekeroğlu 2004; Tsoukanas et al. 2006).

Amblyseius swirskii (Acari: Phytoseiidae) is an omnivorous mite that feeds on many species of small arthropods as well as pollen grains (Swirski et al. 1967; Nomikou et al. 2003; Romeih et al. 2004). It can be introduced as a biological control agent against whiteflies, thrips, spider mites, eriophyid mites and other pests on vegetable crops in greenhouses (Nomikou et al. 2003; Hoogerbrugge et al. 2005; Messelink et al. 2005, 2006). Some studies on development, fecundity and mortality have been conducted (Yousef et al. 1982; Metwally et al. 1984; Hoda et al. 1987; El-Laithy and Fouly 1992; Abou-Awad et al. 1999; Nomikou et al. 2001), but these involved a limited range of temperatures. Our purpose in this study was to develop a comprehensive understanding of the effects of temperature on the population dynamics of *A. swirskii*. These data are necessary to understand and predict the performance of this natural enemy in greenhouse environments.

Materials and methods

Cultures

Colonies of *A. swirski* were initiated from specimens supplied by Koppert Canada (Scarborough, Ontario). Cultures were maintained on plastic arenas, 9 cm in diameter, placed on a wet sponge in a plastic tray containing water in an insectary room. The room was maintained at 25°C, with a 16:8 h photophase:scotophase under fluorescent lamps (Philips Electronics, F32T8, at 1,700 lx). The relative humidity in the room, over the rearing arenas, was approximately 60% RH. Cattail pollen, *Typha latifolia* L. (Typhaceae) was provided as food by dusting it on the arenas twice per week. Pollen was collected from plants in the Fraser Valley, British Columbia, Canada. The pollen was dried, sieved and kept in a freezer at −24°C until use, and was replaced each summer. Plastic tents, 1 cm square, and a few cotton threads were placed on the leaf disc as shelter and oviposition sites, respectively.

Development time, birth rate and death rate

We determined development time, birth rate, and death rate for 100 individual *A. swirskii* from birth to death, under constant temperatures (13, 15, 18, 20, 25, 30, 32, 34 and 36°C) on pepper leaf disc arenas (20 mm diameter). Leaf discs were placed abaxial side up, on water-soaked sponges (23 × 23 × 12 mm) in plastic Petri dishes (35 mm diameter and 25 mm high). The leaf disc arenas were cut from leaves of greenhouse-grown sweet

pepper, *Capsicum anuum* L. (Solanaceae), cv Bell Boy (Stokes Seeds, St. Catherines, Ontario, Canada). Water was added to the arena to keep the leaf disc fresh, and to prevent escape of the mites. Leaf discs were replaced if necessary. Cattail pollen was supplied as food by dusting it on the arenas twice per week. Enough pollen was placed on the arena at each dusting to more than supply the needs of the mite. The experiments were carried out in growth chambers. Light intensity at the level of the arenas was 1,600 lux.

To initiate experiments, groups of gravid adult females placed on pepper leaves with cattail pollen at 1,600 at 25°C, 60% RH. Eggs were transferred singly onto new leaf discs at 0800 the next morning, and this was counted as the start of the experiment. Arenas were placed haphazardly into the different temperature environments until 100 eggs were present in each temperature. The eggs were obtained over time from different groups of adult females. We examined the discs at or below 25°C at 24 h intervals and discs above 25°C 12 h intervals. The developmental stage of each mite was determined at each observation. When the mites became adults, we transferred pairs of newly emerged males and females to individual leaf discs supplied with cattail pollen as above. We counted eggs daily and removed them after the observation. The observations were continued until the mites stopped laying eggs or died. These observations included all of the females that emerged from the development time experiment at each temperature. Additional males were reared at the test temperatures to supply mates if required.

Data and life table analysis

We tested for an effect of temperature on fecundity with a cubic polynomial regression (fecundity $= a + b*$temperature $+ c*$temperature$^2 + d*$temperature^3). We tested for an effect of temperature on longevity of males and females, and on pre-oviposition time with a non-linear regression [$y = a + b*(1/\text{temperature})$]. We tested for effects of temperature on mortality in the immature stages, and on sex ratio, with a logistic regression. These analyses were performed using SYSTAT version 13 (SYSTAT Software 2009, Chicago, IL, USA).

We used the four-parameter, nonlinear developmental equation of Briere et al. (1999), to model the relationship between temperature and development rate. This allowed the estimation of development rate, thermal minima and maxima, and the optimum development temperature. Thus

$$R(T) = aT(T - T_L)(T_U - T)^{(1/m)}$$

where $R(T)$ is development rate (1/days) at a given temperature, T is rearing temperature (°C), a is a scale parameter, T_L is the lower development threshold (°C), T_U is the upper development threshold (°C), and m is an empirical constant, and a shape parameter (Briere et al. 1999). The optimum temperature was computed from the approach given in Briere et al. (1999).

$$T_{\text{OPT}} = (2mT_U + (m + 1)T_L) + \left(4m^2 T_U^2 (m + 1)^2 T_L^2 - 4m^2 T_U T_L\right)^{0.5}/4m + 2$$

The data were fitted to this model using the Marquardt algorithm (Marquardt 1963) with non-linear regression using SYSTAT version 13. The regressions were fitted using the mean values for each temperature.

The life-history data from each temperature were analyzed with an age-stage, two-sex life table (Chi and Liu 1985; Chi 1988), using the computer program TWOSEX (Illinois Natural History Survey 2004). For each temperature, we determined the age-specific

survival rate (l_x), and the age-specific fecundity (m_x), and other stage and age specific parameters as described in Chi and Liu (1985) and Chi (1988). These data were used to determine, also for each temperature, the intrinsic rate of increase (r_m), the finite rate of increase (λ), the net reproductive rate (R_0), the mean generation time (T), the gross reproductive rate (GRR) and the doubling time (DT). The intrinsic rate of increase was estimated by using the iterative bisection method from Goodman (1982):

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

with age indexed from 0. The net reproductive rate was calculated as $R_0 = F(N_f/N)$, where F is the mean fecundity per female, and N_f/N is the proportion of eggs that develop into females (Chi 1988). The mean generation time, T, was defined as the length of time that a population needed to increase to R_0-fold of its size (i. e., $e^{r_m T} = R_0$ or $\lambda^T = R_0$) at the stable age-stage distribution. The mean generation time was calculated as $T = (\ln R_0)/r_m$. The gross reproductive rate (GRR) was calculated as GRR $= \sum m_x$. Doubling time was DT $= \ln (2)/r_m$. Population growth rate, r_m follows a parabolic curve in relation to temperature (Logan et al. 1976; Cloutier et al. 1995), which is similar to development time. We used the four-parameter equation of Briere et al. (1999) to model the relationship between temperature and r_m and to estimate the optimum temperature for population increase.

Results

No hatch of eggs occurred at 13°C, and values from 13°C were not used in any subsequent analysis and modeling. At the remaining temperatures, the development time of all stages, and the longevity, fecundity, adult preoviposition period and total preoviposition period of *A. swirskii* varied with temperature (Table 1). The means of the development times of all stages decreased with increasing temperature until 30°C then increased from 32°C. Fecundity increased with increasing temperature from 15°C, was maximum at 25°C, and then decreased to 36°C (Polynomial Regression, cubic model, $F_{3,514} = 249.45$, $P < 0.0001$). The number of *A. swirskii* completing development ranged from 94 to 100, of 100 eggs initiated at each temperature. Mortality of immature stages of *A. swirskii* was very low at all tested temperatures, and showed no trends with temperature (Logistic Regression, $\chi^2 = 0.24$, $df = 1$, $P = 0.62$). Longevity of females and males, however, decreased with increasing temperature (Non-linear Regression, Longevity $= a + b*$ (1/temperature), Females, $F_{2,514} = 3377$, $P < 0.0001$, Males, $F_{2,252} = 5,201$, $P < 0.0001$). The sex ratio ranged from 0.60 females to 0.76 females, and showed no consistent trend with temperature (Logistic Regression, $\chi^2 = 0.02$, $df = 1$, $P = 0.88$). The preoviposition period decreased with increasing temperatures, in general, reaching a minimum in the range between 30 and 34°C (Non-linear Regression, Longevity $= a + b*$(1/temperature), $F_{2,417} = 346$, $P < 0.0001$).

The four-parameter model (Briere et al. 1999) provided a good fit of the observed development rate values (1/days) over the temperatures (T) at which they were observed (Fig. 1a, $D(T) = 0.0001*T*(T - 8.074)*(37.372 - T)^{1/2.746}$, $R^2 = 0.987$). The lower development threshold was estimated at 8.073 ± 1.121°C, the upper development threshold at 37.372 ± 1.122°C, and the optimum temperature was calculated to be 32.3°C. Curve fitting is presented only for the overall pre-adult development time, although the

Table 1 Means and standard errors of the development time, longevity, fecundity, adult preoviposition period and total preoviposition period of *Amblyseius swirskii* at different constant temperatures

	Temperature (°C)							
	15	18	20	25	30	32	34	36
Egg duration (days)	6.0 ± 0.09	3.8 ± 0.09	3.1 ± 0.05	1.7 ± 0.05	1.1 ± 0.03	1.2 ± 0.04	1.8 ± 0.04	2.0 ± 0.017
(N)	(100)	(100)	(100)	(100)	(100)	(100)	(100)	(100)
Larva duration (days)	3.0 ± 0.05	1.4 ± 0.05	1.3 ± 0.05	1.0 ± 0.01	1.0 ± 0.00	0.8 ± 0.03	0.9 ± 0.02	0.8 ± 0.025
Protonymph (days)	6.9 ± 0.15	5.7 ± 0.13	3.2 ± 0.06	2.3 ± 0.06	2.2 ± 0.05	1.4 ± 0.06	1.6 ± 0.04	1.9 ± 0.066
Deutonymph (days)	7.6 ± 0.18	6.6 ± 0.18	3.3 ± 0.09	2.0 ± 0.06	1.7 ± 0.07	2.1 ± 0.05	1.8 ± 0.08	2.2 ± 0.12
Total Preadult (days)	22.1 ± 0.33	17.5 ± 0.30	10.9 ± 0.13	7.0 ± 0.08	6.0 ± 0.10	5.4 ± 0.09	5.6 ± 0.09	6.9 ± 0.15
Male longevity (days)	62.7 ± 1.90	46.3 ± 1.34	39.2 ± 0.81	29.6 ± 0.36	26.6 ± 0.52	22.2 ± 0.53	21.2 ± 0.29	16.9 ± 0.68
Female longevity (days)	107.8 ± 3.25	55.7 ± 0.58	44.5 ± 0.60	25.8 ± 0.28	21.8 ± 0.46	14.9 ± 0.25	14.5 ± 0.3	15.0 ± 0.39
APOP (days)	83.4 ± 3.74	14.8 ± 1.57	8.9 ± 0.41	4.5 ± 0.12	3.3 ± 0.15	2.6 ± 0.09	2.5 ± 0.08	3.1 ± 0.14
TPOP (days)	107.4 ± 3.65	32.4 ± 1.54	20.3 ± 0.45	11.8 ± 0.16	9.7 ± 0.19	8.2 ± 0.17	8.5 ± 0.12	10.2 ± 0.19
Fecundity (eggs/female)	1.3 ± 0.24 (8a, 1b)	2.6 ± 0.51 (17, 1)	14.9 ± 0.56 (25, 2)	16.1 ± 0.34 (25, 2)	14.5 ± 0.44 (23, 3)	10.1 ± 0.36 (17, 3)	9.5 ± 0.42 (19, 3)	3.3 ± 0.32 (9, 2)
Sex ratio male:female	59:35	71:23	62:35	69:31	60:39	65:31	58:38	72:22
proportion of females	(0.63)	(0.75)	(0.64)	(0.69)	(0.61)	(0.68)	(0.60)	(0.76)

d days, *ATOP* adult preoviposition period, *TPOP* total preoviposition period
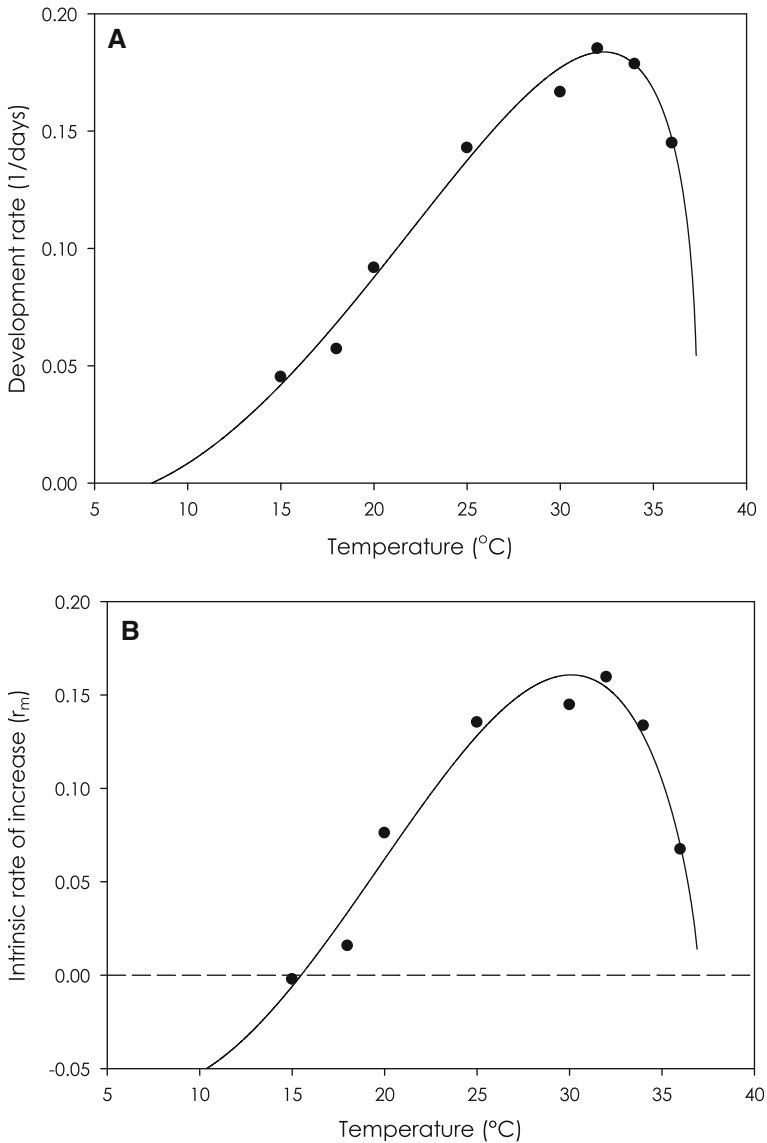
a, Maximum fecundity; b, Maximum daily fecundity

Fig. 1 The relationship between temperature and life history parameters in *Amblyseius swiriskii*. **a** The relationship between temperature and development from egg to adult in *A. swirskii*. The *line* is based on non-linear regression of temperature vs. development rate using the four-parameter model of Briere et al. (1999). The points are the average development time for mites at those temperatures, and are the raw values used in the regression. **b** The relationship between temperature and r_m in *A. swirskii*. The *line* is based on non-linear regression of temperature vs. r_m using the four-parameter model of Briere et al. (1999). The points are the calculated r_m for mites at those temperatures, and are the raw values used in the regression

individual stage data were used to fit stage-specific portions of the life table at the different temperatures and to calculate the population parameters of *A. swirskii* at the different temperatures (Table 2). The intrinsic rate of increase (r_m) at 15°C was −0.0022, suggesting that the *A. swirskii* population will decrease at and below this temperature. The

Table 2 Life table parameters of *Amblyseius swirskii* at different constant temperatures

Temp (°C)	r_{m}	λ	GRR	R_0	T	DT
15	−0.0022	0.9978	2.07	0.77	119.8	−315.0
18	0.0157	1.0158	1.95	1.83	38.5	44.2
20	0.0761	1.0791	9.57	9.22	29.2	9.1
25	0.1353	1.1449	11.18	11.14	17.8	5.1
30	0.1447	1.1557	8.88	8.70	14.9	4.8
32	0.1596	1.1731	6.83	6.63	11.8	4.3
34	0.1336	1.143	5.77	5.50	12.8	5.2
36	0.0674	1.0697	2.51	2.36	12.8	10.3

Intrinsic rate of increase (r_{m})

Finite rate of population increase (λ)

Gross reproduction rate (GRR)

Net reproductive rate (R_0)

Mean generation time (T)

Doubling Time (DT)

intrinsic rate of increase and the finite rate of population increase (λ) were greatest at 32°C. The gross reproductive rate (GRR) and net reproductive rate (R_0) were greatest 25°C. The mean generation time (T) was shortest at 34 and 36°C, and the doubling time (DT) was shortest at 32°C. The negative doubling time at 15°C reflects the time required for the population to decrease by half.

The 4-parameter model (Briere et al. 1999) provided a good fit to the observed r_{m} over the temperatures at which it was determined (Fig. 1b) ($r_{\mathrm{m}}(T) = 0.0000943*T*(T − 15.486)*(36.992 − T)^{1/1.425}$, $R^2 = 0.95$). The estimate of the lower threshold for positive growth (the lower x-intercept) was 15.49 ± 0.905°C and for the upper threshold for positive growth (the upper x-intercept) was 36.99 ± 0.816°C. The calculated optimum temperature (T_{opt}) based on this regression was 30.09°C. Below 15.49°C and above 36.99°C, the growth of *A. swirskii* populations feeding on pollen of *T. latifolii* should be negative.

Discussion

Our results demonstrate that *A. swirskii* can develop and reproduce successfully over a range of temperatures from 15 to 36°C, with little developmental mortality at any of the temperatures tested (Table 1). However, the life-table parameters derived from these data demonstrate that the rate of population increase will be vastly different over this range of temperatures (Table 2). Negative population growth would occur below 15.5°C, and above 37°C (Table 2; Fig. 1b). Moreover, values for the generation time (T) and doubling time (DT) suggest that substantial and rapid population increases would only occur above 20°C. This has implications for the performance of *A. swirskii* as a biological control of insect pests in greenhouses.

In greenhouse peppers in British Columbia, for example, the desired average daily temperature through the year is in the range of 15–25°C, with the actual setpoints and ranges being determined by available light, plant age and season (British Columbia

Greenhouse Growers' Association and Province of British Columbia Ministry of Agriculture, Food and Fisheries 2005). During the winter months, average daily temperatures are usually in the range of 20°C or less. These temperatures would result in slow population growth of *A. swirskii*, and might allow target pests to escape from regulation if *A. swirskii* was the only control agent, and if the population growth of prey species was proportionately less affected by low temperatures. The escape of pest populations from regulation by natural enemies at moderate production temperatures is known for *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) attacking twospotted spider mites, *Tetranychus urticae* Koch (Acari: Tetranychidae) (Stenseth 1979) and for *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) attacking greenhouse whiteflies, *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae) (Hulspas-Jordaan et al. 1987). The development rate of the greenhouse whitefly, in relation to temperature has a shallow slope, relative to that of *A. swirskii*, and significant oviposition occurs below 20°C (van Roermund and van Lenteren 1992). Therefore, biological control of greenhouse whitefly by *A. swirskii*, might be quite sensitive to temperature. The development rate for western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) has a moderately steep slope in relation to temperature. Development, oviposition and r_m of *F. occidentalis* are substantially reduced below 20°C (Katayama 1997), and population growth overall is reduced below 20°C (Nothnagl et al. 2008). Thus, the temperature responses of *A. swirskii* and *F. occidentalis* appear quite similar. The r_m in relation to temperature, for *Amblyseius cucumeris* (Oudemans) (Acari: Phytoseiidae), as shown by Cloutier et al. (1995), is very similar to that of *A. swirskii*. Given the widespread success of *A. cucumeris* for biological control of thrips, the effects of temperature on population growth of *A. swirskii* may not be a concern in biological control programs emphasizing *F. occidentialis* but may be a concern if *T. vaporariorum* is the target. It should be pointed out that our studies were conducted at constant temperatures. Studies conducted under fluctuating temperatures can produce somewhat different results (Hagstrum and Milliken 1991; Easterbrook et al. 2003).

We started our development time studies with eggs produced at 25°C and the average age of these was 8 h when they were placed in experimental conditions. The interval preceding placement in the experimental conditions was not included in our analysis. Our results thus underestimate development time for eggs at temperatures below 25°C and overestimate development time at temperatures above 25°C. For development times of eggs, this introduces a significant error. We estimated the lower threshold for development from egg to adult in *A. swirskii*, which is a warm-climate, Mediterranean species (Nomikou et al. 2001), to be 8.1°C. This is low, considering the species' Mediterranean origins, and is similar to the thresholds estimated for temperate climate species (Campbell et al. 1974; Trudgill et al. 2005). However, the threshold levels in the preceding citations are based on linear regression within the "straight-line" portion of the temperature curve. Using linear regression on the points from 15 to 30°C yields a lower development threshold estimate of 9.8°C. The point at 30°C is close to the inflection point for the curve, and assuming it is not in the straight-line portion of the curve, a linear regression using the points from 15 to 25°C, then yields a lower development threshold estimate of 11.3°C. Given that we were unable to detect development in eggs at 13°C, and that the threshold for positive population growth was estimated at 15.5°C, the higher threshold estimates are likely more realistic.

The population dynamics of *A. swirskii* varied with temperature from 15 to 36°C (Table 2). The net reproductive rate was greatest at 25°C, but r_m was greatest, and doubling time least, at 32°C. The r_m of *A. swirskii* feeding on immatures of *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) at 25°C was 0.213 and 0.208 for two different

strains of Mediterranean origin (Nomikou et al. 2001). The methods used by these authors to determine r_m overestimates true value (Nomikou et al. 2001). The r_m for *A. swirskii* feeding on *F. occidentalis* and *Thrips tabaci* at 25°C was 0.056 and 0.024, respectively (Wimmer et al. 2008), although these authors noted that high mortality of immatures was responsible for the low r_m. They calculated an r_m of 0.138 and 0.139, respectively when immature mortality was excluded (Wimmer et al. 2008), which is close to our estimate of 0.145 at 25°C. El-Laithy and Fouly (1992) estimated an rm of 0.167 for *A. swirskii* feeding on *T. urticae* at 26°C. This is somewhat greater than our estimate, and the higher value may reflect feeding on animal prey versus plant pollen (Abou-Awad et al. 1992). Abou-Awad et al. (1999) estimated an r_m of 0.155 and 0.122 for *A. swirskii* feeding on the eriophyid mites *Aceria ficus* (Cotte) and *Rhynacaphytoptus ficifoliae* Kiefer (Acari: Eriophyidae), respectively, at 29°C, which is very close to our estimate at 30°C. Overall, feeding on pollen of *T. latifolia* seems to result in a slightly lower rate of population increase, but values obtained by others are generally in the same range as ours, at similar temperatures.

Yousef et al. (1982) reported development times of 19.3 days at 15°C and 5.2 days at 30°C, with a diet of *T. urticae*. These durations are considerably shorter than ours, and this may reflect the effects of food (*T. urticae* vs. *T. latifolia* pollen), or differences in the populations. Park et al. (2010) found a development time of 6.2 days for *A. swirski* females fed on cattail pollen, at 25°C, which is also somewhat shorter that the duration we recorded at that temperature. Wimmer et al. (2008) found a development time of 7.8 days when *A. swirskii* were fed on a diet of either *F. occidentalis* or *Thrips tabaci* Lindeman (Thysanoptera: Thripidae) at 25°C. El-Laithy and Fouly (1992) report a total development time of 3.84 days for female *A. swirskii* developing at 26°C on a diet of *T. uriticae*; however, the sum of immature development times reported by these authors is 5.67 days, which is similar to other reports but still shorter than our observations. Abou-Awad et al. (1992) reported generation times, at 27°C, of 13.25 and 19.15 days on diets of *T. urticae* and pollen of *Ricinus communis* L. (Euphorbiaceae), respectively. These are in the range of our calculated generation times of 17.8 and 14.9 days at 25 and 30°C, respectively. With the exception of Wimmer et al. (2008), our development times appear substantially longer than those found by others. It is not clear why this should be so.

Our results provide a comprehensive evaluation of the effects of temperature on the population dynamics of *A. swirskii*. This will allow parameterization of models that will allow the evaluation of the effects of temperature on performance of *A. swirskii* as a biological control agent, and provide a basis for development of improved strategies for using this mite in biological control programs.

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