

Effect of temperature on population growth and life table parameters of *Nephus arcuatus* (Coleoptera: Coccinellidae)

SARA ZARGHAMI¹, FARHAN KOCHEILI¹, MOHAMMAD S. MOSSADEGH¹, HOSSEIN ALLAHYARI²
and ARASH RASEKH¹

¹Shahid Chamran University of Ahvaz, Department of Plant Protection, Ahvaz, Khuzestan, Islamic Republic of Iran; e-mails: s-zarghami@phdstu.scu.ac.ir; kocheilif@yahoo.com; mossadegh_ms@yahoo.com; arashrasekh@gmail.com

²University of Tehran, Department of Plant Protection, Karaj 98511-2413270, Islamic Republic of Iran; e-mail: allahyar@ut.ac.ir

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Abstract. The development, reproduction and life table parameters of the predator *Nephus arcuatus* Kapur (Coleoptera: Coccinellidae), the most important predator of the spherical mealybug, *Nipaeococcus viridis* (Newstead) (Homoptera: Pseudococcidae) were studied at five constant temperatures (15, 20, 25, 30 and 35 ± 1°C, 65 ± 5% RH and a photoperiod of 14L: 10D). The duration of total pre-adult stage was found to decrease with increase in temperature from 60.0 days at 20°C to 15.3 days at 35°C. The oviposition period lasted 58.5, 44.7, 53.2 and 24.5 days at 20, 25, 30 and 35°C, respectively, with females laying an average of 164.8, 415.2, 660.4 and 136.6 eggs, respectively, at these four temperatures. Life table data were analyzed using an age-stage, two-sex life table. The intrinsic rate of increase ($r_m = 0.1540 \text{ d}^{-1}$), finite rate of increase ($\lambda = 1.1666 \text{ d}^{-1}$) and net reproductive rate ($R_0 = 197.9$ offspring) were greatest at 30°C. The shortest mean generation time ($T = 30.6$ days) was recorded at 35°C. These results indicate that *N. arcuatus* can successfully survive and reproduce at temperatures of around 30°C and has the potential to be an effective biological control agent of *N. viridis* and other mealybugs in warm regions.

INTRODUCTION

This study concerns one of the most effective predators of mealybugs in warm regions, namely the recently described *Nephus arcuatus* Kapur (Coleoptera: Coccinellidae), which is indigenous to warm regions of Southwestern Iran (Löbl & Smetana, 2007). It also occurs in Yemen and Saudi Arabia (Ramindo & van Harten, 2000). This small coccinellid has a high searching capacity, especially in warm regions and is an important biological control agent of the spherical mealybug, *Nipaeococcus viridis* (Newstead) in orchards in Dezful, Southwestern Iran.

N. viridis is a polyphagous pest, which feeds on a wide range of ornamental plants and orchards crops throughout tropical and subtropical regions and a large part of the Pacific Basin (Sharaf & Meyerdirk, 1987; Nechols, 1995) and occurs in South and Southwestern Iran (Moghadam, 2006). Symptoms of plants infested with *N. viridis* are curling and dwarfing of terminal growth, abortion of flowers, yellowing of leaves and abortion of fruit. Indirect damage results from production of sticky honeydew that facilitates the growth of black mould and reduces plant growth (Abdul-Rassoul, 1970; Sharaf & Meyerdirk, 1987; Al-Rawy et al., 1997). Chemical control of mealybugs is often ineffective because they tend to live in protected locations and are also protected by the mealy wax covering their eggs and body (Joyce et al., 2001). In contrast, mealybugs are controlled by releases of either a single predator (Mani & Thontadarya, 1989; Afifi et al., 2010) or parasitoid (Meyerdirk et al., 1988; Muniappan et al., 2006; Amarasekare et al., 2009), or of both (Kairo et al., 2000; Abd-Rabou, 2008).

Currently in Iran, *Cryptolaemus montrouzieri* Mulsant is used for the biological control of mealybugs in orchards and greenhouses. In some regions, however, probably due to unsuitable weather, lack of alternative prey (DeBach & Hagen, 1964; Izhevsky & Orlinsky, 1988; Yigit & Canhilal, 1998) and the ants that attend mealybugs (Hernandez et al., 1999; Mossadegh et al., 2008b), this predator is not able to establish itself and is mass-reared and released each year in order to control mealybugs.

The use of a natural enemy to control a pest should be based on a comprehensive life table study of its natural enemies. In the case of coccinellids both males and females kill and eat prey and it is therefore important to include the effects of both sexes when evaluating their effectiveness as biological control agents. Female age-specific life table (Lewis, 1942; Leslie, 1945; Birch, 1948; Carey, 1993) deal only with female populations and ignores the variable developmental rates of individuals, stage differentiation and males in a population. In contrast, age-stage, two-sex life table developed by Chi & Liu (1985) and Chi (1988) takes these factors into consideration. This type of life table has been used to describe the population characteristics of many insects and their natural enemies (Chi & Yang, 2003; Gabre et al., 2005; Yu et al., 2005, 2013; Chi & Su, 2006; Huang & Chi, 2013).

Understanding the effect of the main abiotic factor, temperature, on the development and fecundity of *N. arcuatus* could be a useful way of predicting the activity and population dynamics of this predator in the field and of optimizing mass rearing under laboratory conditions. In the present

study the effect of temperature on the population growth rate and life table parameters of *N. arcuatus* feeding on *N. viridis* was determined.

MATERIAL AND METHODS

Insect culture

The spherical mealybug, *N. viridis* was mass reared on potato sprouts (*Solanum tuberosum*) in boxes (24 × 16 × 10 cm) tightly covered by a fine mesh net. Adults of *N. arcuatus* were originally collected from an orchard infested with *N. viridis* in Dezful (48°30'E, 32°20'N), Khuzestan province, Southwestern Iran in April 2010. *N. arcuatus* adults were placed in rearing boxes containing sprouted potatoes infested with *N. viridis*. These boxes were checked daily and fresh infested sprouts were added as needed. The stock colonies of *N. arcuatus* and *N. viridis* was maintained in an incubator at 25 ± 1°C, 65 ± 5% RH and 14L : 10D photoperiod for three generations before they were used in the experiments. To maintain genetic variability, adults of *N. arcuatus* were field collected and mixed with the stock every few months.

Biology and life table parameters

This study was conducted at 5 constant temperatures: 15, 20, 25, 30 and 35 ± 1°C, 65 ± 5% RH and a photoperiod of 14L : 10D. Before initiating the experiment, a colony of the coccinellid was maintained at either 15, 20, 25, 30 or 35°C, 65 ± 5% RH and a photoperiod of 14L : 10D for one generation. To have a cohort of eggs of the same age (< 8 h), 50 paired *N. arcuatus* were obtained from the stock population kept at each temperature and were released into a colony of mealybugs in a cylindrical container (18 × 8 cm) covered with fine mesh net for ventilation. Eight hours later, 100 eggs were removed and placed in Petri dishes (6 × 1 cm), individually in order to avoid cannibalism, and were maintained under the same conditions in which they were laid. Newly emerged larvae were transferred to individual plastic containers (3 × 3 cm), containing 1.5% agar where they were reared on a piece of sprouted potato infested with *N. viridis* that had been placed upside down in the middle of the container. Observations were made daily. Larval development and mortality were assessed every 12 h. After the emergence of adults, males and females were paired and checked daily to record survival and fecundity.

Statistical analysis

The developmental time of individuals, both male and female, and those dying before reaching the adult stage and the fecundity of *N. arcuatus* at different temperatures were analyzed using an

age-stage, two-sex life table (Chi & Liu, 1985) and following the procedure described by Chi (1988). The adult pre-oviposition period (APOP) (the duration from adult emergence to first oviposition) and total pre-oviposition period (TPOP) (the duration from egg to first oviposition) were calculated. The population parameters (net reproductive rate (R_0), intrinsic rate of increase (r), finite rate of increase (λ) and mean generation time (T) were also calculated. The age-stage life expectancy (e_{xy}) was calculated according to Chi & Su (2006). The intrinsic rate of increase (r_m) was estimated using the iterative bisection method and Euler-Lotka equation with age indexed from 0 (Goodman, 1982):

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

The finite rate of increase (λ), net reproductive rate (R_0) and mean generation time (T) were calculated as follows:

$$\lambda = e^r \quad (2)$$

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \quad (3)$$

$$T = \frac{\ln R_0}{r_m} \quad (4)$$

The relationship between the net reproductive rate (R_0) and mean female fecundity (F) based on the two-sex life table is that provided by Chi's (1988) equation:

$$R_0 = \frac{N_f}{N} \quad (5)$$

Where N is the total number of eggs (100) used in the life table study and N_f the number of female adults developed from N eggs. Data analysis and population parameters (Chi, 1988; Chi & Liu, 1985) were calculated using the TWOSEX-MSChart computer program (Chi, 2012). To estimate the means, variances and standard errors of the population parameters, bootstrap techniques were used (Erfon & Tibshirani, 1993). To generate less variable results, 10,000 iterations were performed (Yu et al., 2013). We used the Tukey-Kramer test (Dunnett, 1980) to compare the differences among treatments.

RESULTS

N. arcuatus did not lay eggs at 15°C, so only its biological characteristics at 20, 25, 30 and 35°C are recorded (Table 1). Out of the cohort of 100 eggs at the beginning of each experiment, 84, 94, 91 and 68 eggs hatched at 20,

TABLE 1. Mean (± SEM) developmental time and pre-adult mortality of *N. arcuatus* fed on *N. viridis* at four constant temperatures.

Statistic parameters	Temperature							
	20°C		25°C		30°C		35°C	
	mean ± SE	n	mean ± SE	n	mean ± SE	n	mean ± SE	n
Developmental time (days)*								
Egg	12.1 ± 0.1 a	84	6.4 ± 0.1 b	94	3.9 ± 0.0 c	91	3.6 ± 0.0 c	68
1st instar	7.1 ± 0.1 a	78	3.9 ± 0.0 b	80	2.2 ± 0.0 c	86	1.8 ± 0.0 d	59
2nd instar	5.6 ± 0.1 a	71	2.5 ± 0.0 b	78	1.3 ± 0.0 c	86	1.2 ± 0.0 c	58
3rd instar	6.2 ± 0.1 a	67	2.8 ± 0.0 b	77	1.5 ± 0.0 c	85	1.5 ± 0.0 c	57
4th instar	11.9 ± 0.2 a	52	4.7 ± 0.1 b	74	2.6 ± 0.0 c	82	2.7 ± 0.1 c	54
Pre-pupa	4.2 ± 0.1 a	48	2.2 ± 0.1 b	71	1.0 ± 0.0 c	82	1.1 ± 0.0 c	49
Pupa	13.2 ± 0.2 a	44	7.1 ± 0.1 b	68	5.1 ± 0.1 c	78	3.6 ± 0.1 d	46
Total pre-adult	60.0 ± 0.5 a	44	29.5 ± 0.2 b	78	17.6 ± 0.1 c	78	15.3 ± 0.1 c	46
Total pre-adult mortality (%)	56%	56	32%	32	23%	23	54%	54

* Values in rows followed by the same letter are not significantly different based on a Tukey-Kramer test with $\alpha = 0.05$.

TABLE 2. Mean (\pm SEM) preoviposition period (APOP), total preoviposition period (TPOP), oviposition period, adult longevity and fecundity of *N. arcuatus* fed on *N. viridis* at four constant temperatures.

Statistics	Temperature							
	20°C		25°C		30°C		35°C	
	mean \pm SE	<i>n</i>	mean \pm SE	<i>n</i>	mean \pm SE	<i>n</i>	mean \pm SE	<i>n</i>
Adult longevity (days)								
Female	157.3 \pm 12.6 a*A**	25	93.8 \pm 10.7 bA	23	116.5 \pm 6.6 bA	30	44.6 \pm 4.2 cA	24
Male	144.4 \pm 13.0 aA	19	121.8 \pm 10.1 bA	45	86.1 \pm 6.3 cB	48	42.4 \pm 2.6 dA	22
Adult preoviposition (days)								
APOP	11.6 \pm 0.8 a	20	5.8 \pm 0.3 b	22	4.2 \pm 0.1 c	30	3.4 \pm 0.4 c	20
TPOP	70.1 \pm 1.2 a	20	35.5 \pm 0.3 b	22	21.9 \pm 0.2 c	30	18.7 \pm 0.4 d	20
Oviposition days (days)	58.5 \pm 1.2 a	20	44.7 \pm 1.4 b	22	53.2 \pm 0.6 b	30	24.5 \pm 0.7 c	20
Fecundity (egg/female)	164.8 \pm 25.0 c	25	415.2 \pm 57.8 b	23	660.4 \pm 37.9 a	30	136.6 \pm 24.0 c	24
Maximum daily fecundity	15		29		32		22	

Values in rows with the same small* letters are not significantly different based on a Tukey-Kramer test with $\alpha = 0.05$. Values in columns (for longevity) with the same capital** letters are not significantly different based on a Tukey-Kramer test with $\alpha = 0.05$.

25, 30 and 35°C, respectively. The total developmental time from egg hatch to adult emergence decreased significantly with increase in temperature, with the longest period recorded at 20°C and shortest at 35°C. The lowest total pre-adult mortality occurred at 30°C followed by that at 25, 20 and 35°C, respectively. The adult pre-oviposition period (APOP), total pre-oviposition period (TPOP) and oviposition period decreased significantly with increase in temperature. Fecundity was highest at 30°C and lowest at 35°C (Table 2). Adult longevity at 20°C was significantly longer than that of adults reared at other temperatures. For all temperatures except 25°C, females lived longer than males but not significantly so.

The age-stage specific survival rate (s_{xy}) curve of *N. arcuatus* indicates the probability of a newborn larva surviving to age x and stage j (Fig. 1). Due to the variation in the developmental rates between individuals there are overlaps in the stage survival rate. The probability that a newly laid egg will develop to the adult stage increases with increase in temperature between 20 and 30°C and then decreases at 35°C. Both females and males developing at 20°C survived longer than those developing at other temperatures (Fig. 1). Because greater numbers of females survived than males, the proportion of females was greater at all temperatures except 25°C.

The age-specific survival rate (l_x) decreased with increasing temperature. In contrast, the percentage of time females spent ovipositing increased with increase in temperature. The highest peaks for age-stage specific fecun-

dity [f_{x8} (i.e. the female is the eight life stage)], age-specific fecundity (m_x) and age specific maternity ($l_x m_x$) were recorded at 30°C (Fig. 2).

The negative effect of a decrease in temperature on reproduction in *N. arcuatus* can be observed in the age-specific reproductive curve (v_{xy}). The maximum reproductive peak of females reared at 20°C occurred much later than that of females reared at 30°C (Fig. 3).

The age-stage specific life expectancy (e_{xy}) of a newborn (e_{01}) is exactly the same as the mean longevity. The maximum life expectancy of all stages of *N. arcuatus* was recorded at 20°C (Fig. 4). Life expectancy decreased gradually with age since the study was conducted in the laboratory and thus unaffected by adverse effects of field conditions.

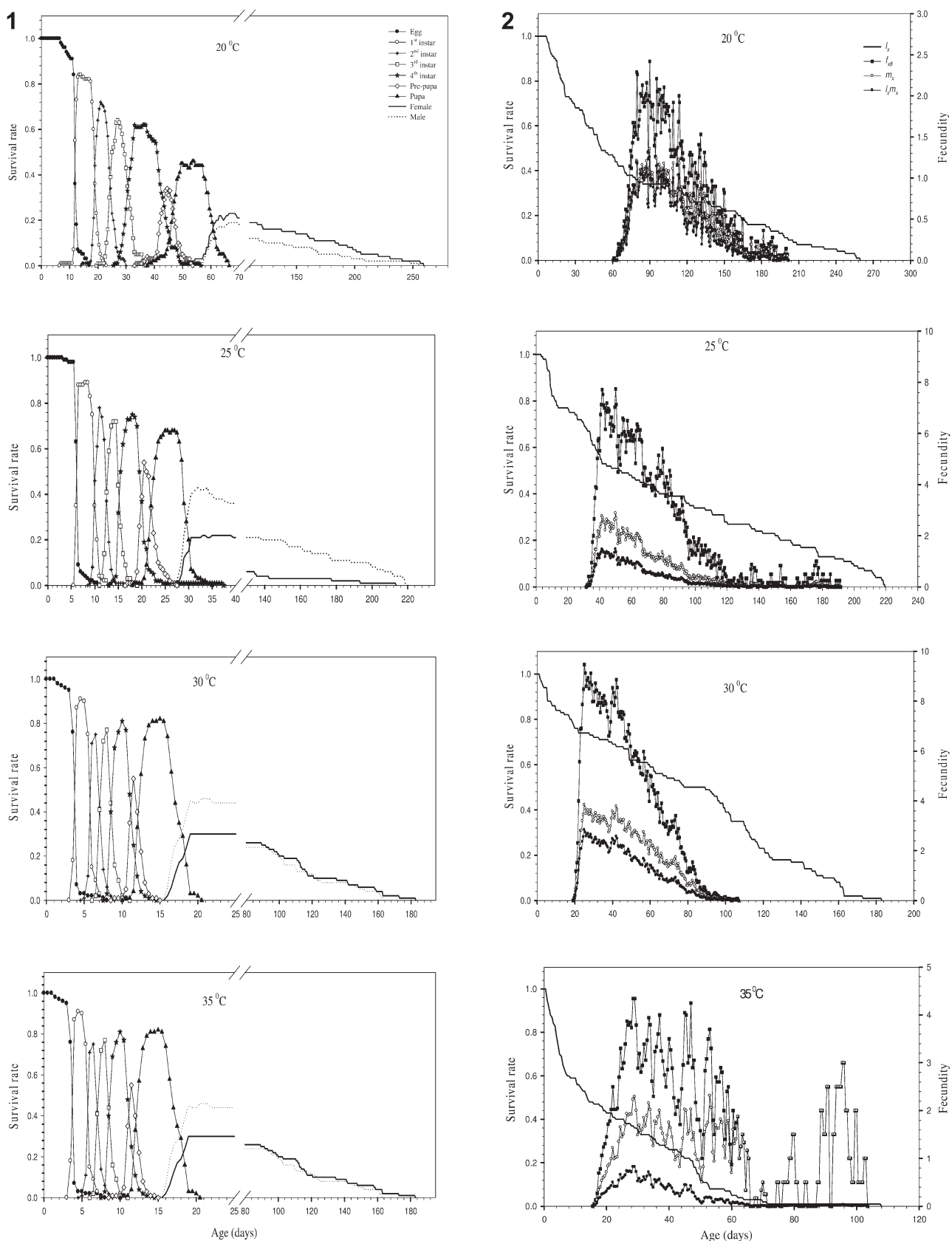
The mean and standard errors of the population parameters are presented in Table 3. Temperature had a significant effect on intrinsic rate of increase (r_m). Increasing values of 0.0377, 0.0878 and 0.1540 d⁻¹ were recorded at 20, 25 and 30°C, respectively. At 35°C, however, there was a reduction in the value to 0.1132 d⁻¹. The rate of population growth was greatest at 30°C and lowest at 20°C. The finite rate of increase was greatest at 30°C. The longest mean generation time was recorded at 20°C and the shortest at 35°C. The highest net reproductive rate (R_0) was recorded at 30°C.

All of our results for *N. arcuatus* reared at different temperatures are consistent with the relationships of equation 5. If a life table is constructed based on adult age and ig-

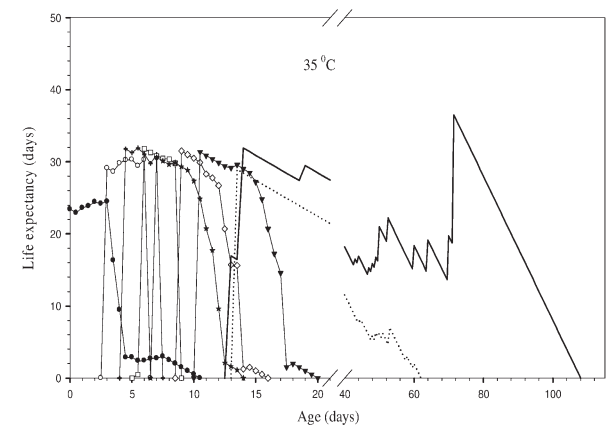
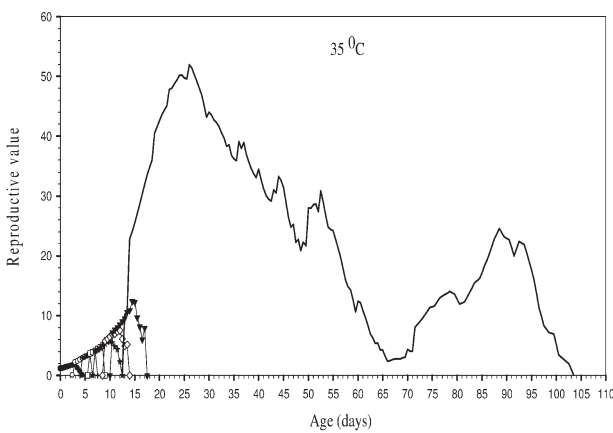
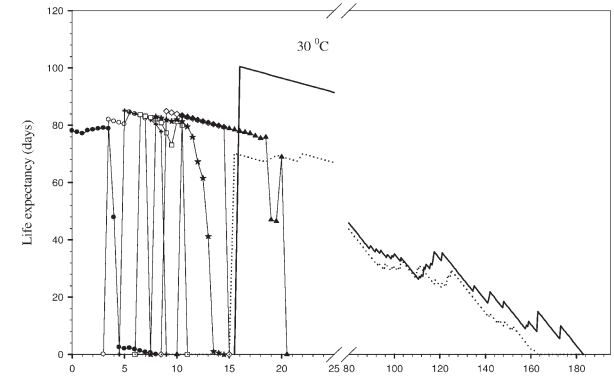
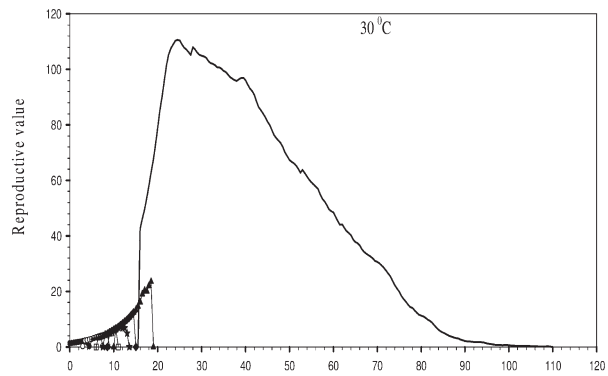
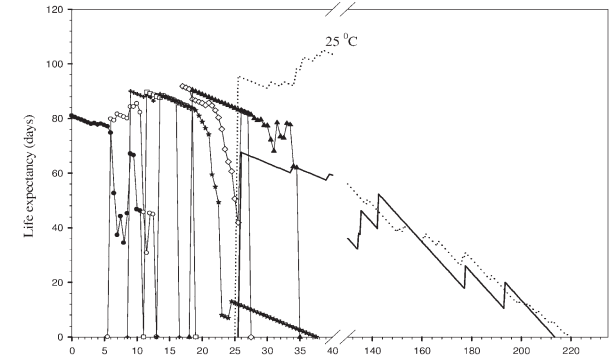
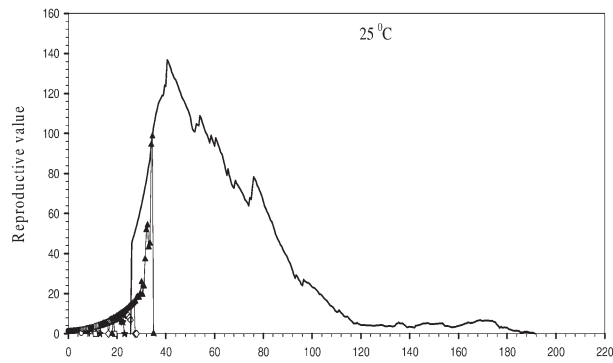
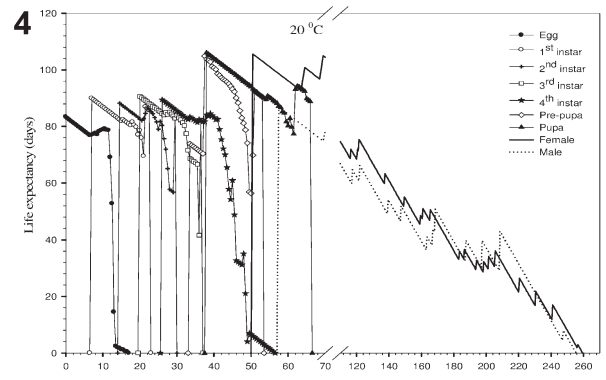
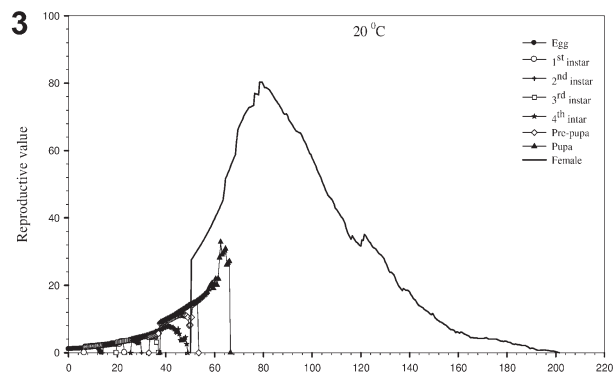
TABLE 3. Mean (\pm SEM) population parameters of *N. arcuatus* fed on *N. viridis* at four constant temperatures.

Parameters	Temperature			
	20°C	25°C	30°C	35°C
r (days ⁻¹)	0.0377 \pm 0.0026 d	0.0878 \pm 0.0047 c	0.1540 \pm 0.0056 a	0.1132 \pm 0.0094 b
λ (days ⁻¹)	1.0386 \pm 0.0027 d	1.0918 \pm 0.005 c	1.1666 \pm 0.0067 a	1.1199 \pm 0.0105 b
R_0 (offspring)	41.2 \pm 9.1 c	95.4 \pm 21.6 b	197.9 \pm 32.2 a	32.6 \pm 8.0 c
T (days)	97.6 \pm 1.7 a	51.5 \pm 1.1 b	34.1 \pm 0.4 c	30.6 \pm 0.7 c

Values in rows with the same small letter are not significantly different based on a Tukey-Kramer test with $\alpha = 0.05$.



Figs 1–2. 1 – age-stage specific survival rate (s_{xj}) calculated for *N. arcuatus* fed on *N. viridis* at four constant temperatures; 2 – age-specific survival rate (l_x), age-stage specific fecundity (f_{x8}), age-specific fecundity (m_x) and age-specific maternity ($l_x m_x$) calculated for *N. arcuatus* fed on *N. viridis* at four constant temperatures.



Figs 3–4. 3 – age-specific reproductive value (v_{xj}) calculated for *N. arcuatus* fed on *N. viridis* at four constant temperatures; 4 – age-stage life expectancy (e_{xj}) calculated for *N. arcuatus* fed on *N. viridis* at four constant temperatures.

nores pre-adult mortality, it will provide an erroneous relationship between mean fecundity and net reproductive rate (Chi & Yang, 2003; Yu et al., 2005; Chi & Su, 2006).

DISCUSSION

One of the main factors influencing the biology, ecology and dynamics of pests and their natural enemies, is temperature (Jervis & Copland, 1996). In the southwest of Iran the climate is hot and dry, which is suitable for mealybugs (Moghadam, 2006; Mossadegh et al., 2008a, 2012; Alizadeh et al., 2013). *C. montrouzieri*, a predator of mealybugs, was introduced into this region and is often released into orchards to control *N. viridis*. This predator is native to Australia and adapted to tropical climates (Gautam & Parasram, 1996). The optimum temperature for its development is reported to be 30°C (Babu & Azam, 1987) and temperatures above 42°C are lethal after even a short period (Solangi et al., 2013). In Southwestern Iran only one spring generation is possible and, as the temperature during summer is very high, its reproduction and other activities are suppressed (Mossadegh et al., 2008a). Although the average temperatures in this region ranged from 36.7°C in July to 35.6°C in August over the period 2008 to 2012, high densities of *N. arcuatus* were observed in orchards and on ornamental plants infested with mealybugs (authors field observation). *N. arcuatus* is considered to be the most effective predator of *Maconellicoccus hirsutus* Green, because it is abundant and active for long periods of the year, especially during the hot summer months. For these reasons Alizadeh et al. (2013) introduced it into Ahvaz in Southwestern Iran. In the study reported here we found that an increase in temperature led to a reduction in the developmental period of pre-adult stages of *N. arcuatus*. Our results are similar to those of Canhilal et al. (2001) and Kontodimas et al. (2007) for other species of *Nephus*. The survival of pre-adult stages was greatest and pre-adult mortality least at 30°C. At 30°C the mortality rate of the immature stages of *Nephus includens* Kirsch is lowest (34.4% mortality) and highest at 35°C (71.6% mortality) (Canhilal et al., 2001). In our study pre-adult mortality at 35°C was lower, indicating that *N. arcuatus* is less sensitive than *N. includens* to temperatures above 30°C. The females were most fecund at 30°C and more fecund than values reported for other pseudococcid predators such as *N. includens* (162.8 eggs), *Nephus bisignatus* Boheman (96.88 eggs) (Kontodimas et al., 2007), *Nephus kreissli* Fürsch & Uygün (122.6 eggs) (Mustu & Klincer, 2013), *Nephus reunioni* Fürsch (177.1 eggs) (Izhevsky & Orlinsky, 1988) and *C. montrouzieri*, the key competitor in controlling mealybugs (510 eggs) (Fand et al., 2010) and (486.9 eggs) (Solangi et al., 2012).

Fisher (1958) defines the reproductive value as the contribution of an individual to the future population. The earlier occurrence of the reproductive peak at 30°C shows that increasing the temperature from 20 to 35°C resulted in an increase in the rate of increase of the population. Because the life expectancy value is calculated using the age-stage survival rate (s_{xj}), which does not assume the population

reaches a stable age-stage distribution, it can be used to predict the survival of a population (Chi & Su, 2006). By using life expectancy we can predict that both males and females of *N. arcuatus* can be expected to live for more than 5 months or 1 month at 20 and 35°C, respectively. However, this value could be different under field conditions where both biotic and abiotic factors vary. Solangi et al. (2013) report that *C. montrouzieri* can survive 33.13 days at 35°C, which is substantially shorter than *N. arcuatus* can survive at the same temperature.

The life table is a useful tool for evaluating the effectiveness of natural enemies for controlling pests under various climatic conditions and in different habitats (Birch, 1948; Jervis & Copland, 1996). Among life table parameters (R_0 , r_m , λ , T), the r_m parameter is especially interesting because it integrates mortality and fertility into a single value. The maximum intrinsic rate of increase for *N. arcuatus* feeding on *N. viridis* was recorded at 30°C and is greater than the value for *N. kreissli* feeding on *Planococcus citri* Risso at 28°C ($r_m = 0.0709$) (Mustu & Klincer, 2013), *N. includens* feeding on *P. citri* at 30°C ($r_m = 0.086$), *N. bisignatus* feeding on *P. citri* at 25°C ($r_m = 0.060$) (Kontodimas et al., 2007) and *C. montrouzieri* feeding on *P. citri* ($r_m = 0.092$) (Ghorbanian et al., 2011) or *M. hirsutus* ($r_m = 0.135$) at 27°C (Persad & Khan, 2002).

Based on our results the optimal temperature for population growth of *N. arcuatus* is 30°C. Because it has a greater survival and longevity, higher reproductive capacity and voracious appetite, and can feed on a wide range of prey than other pseudococcid predators, we conclude that it should be possible to introduce and use *N. arcuatus* as an effective biological control agent of mealybugs in regions with the same climatic conditions as the southwestern part of Iran.

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