Temperature-Dependent Development and Demography of *Scymnus subvillosus* (Coleoptera: Coccinellidae) Reared on *Hyalopterus pruni* (Homoptera: Aphididae)

REMZI ATLIHAN[1] AND HSIN CHI[2]

ABSTRACT   The development, survival, and fecundity of *Scymnus subvillosus* (Goeze) (Coleoptera: Coccinellidae) were studied at 20, 25, 30, and 35°C, 60 ± 5% RH, and a photoperiod of 16:8 (L:D) h (5,000 lux) under laboratory conditions. The total developmental time from egg hatch to adult eclosion ranged from 22.6 d at 20°C to 10.6 d at 35°C. The developmental rates of the egg stage, the larval stage, and total preadult stage at different temperatures increased linearly with increasing temperature. The thermal summation of the egg stage, the larval stage, and the total preadult stage was 77.5, 145.8 and 300 degree-days (DD), respectively. The developmental threshold of the egg stage, the larval stage, and the total preadult stage was 7.4, 4.1, and 7.1°C, respectively. The life history raw data were analyzed using the age-stage, two-sex life table. The intrinsic rate of increase was 0.0845, 0.1138, 0.1395, and 0.0668 d^{-1} at 20, 25, 30, and 35°C, respectively. The net reproductive rate was highest at 25°C ($R_0 = 78.7$), and lowest at 35°C ($R_0 = 4.7$). The mean generation time was shortest at 35°C ($T = 23.9$ d). The life table data can be used for the projection of population growth and designing mass rearing programs.

ÖZET *Scymnus subvillosus* (Goeze) (Coleoptera: Coccinellidae)'un dört farklı sıcaklık (20, 25, 30, ve 35°C), % 60 ± 5 orantılı nem ve 16 saat aydınlatmalı (5000 Lüx) laboratuvar koşullarında gelişme, canlı kalma oranı ve üremesi incelenmiştir. Yumurtadan ergine gelişme süresi 22.6 gün (20°C) ile 10.6 gün (35°C) arasında değişmiştir. Yumurta ve larva dönemleri ile toplam ergin öncesi dönemin gelişme oranı sıcaklıktaki artışla birlikte doğrusal olarak artmıştır. Yumurta, larva ve toplam ergin öncesi dönemlerin gelişmesi için gereksinim duyulan etkili sıcaklıklar toplamı sırasıyla 77.5, 145.8 ve 300 gün-derece, bu dönemlerin gelişme eşiği sıcaklıkları ise sırasıyla 7.4, 4.1, ve 7.1°C olarak hesaplanmıştır. Elde edilen verilerden yaşa bağlı, iki eşeyli yaşam çizelgesi analizi ile yaşam çizelgesi parametreleri oluşturulmuştur. Avcının kalıtsal üreme yeteneği değerleri 20, 25, 30, ve 35°C de sırasıyla 0.0845, 0.1138, 0.1395 ve 0.0668 gün^{-1} olarak bulunmuştur. En yüksek net üreme gücü değeri 25°C de ($R_0 = 78.7$), en düşük ise 35°C de ($R_0 = 4.7$) elde edilmiştir. En kısa ortalama döl süresi değeri 35°C de ($T = 23.9$ gün) elde edilmiştir. Bu çalışma sonucunda elde edilen yaşam çizelgesi verilerinin avcının populasyon gelişmesinin tahmininde ve kitle üretim programının düzenlenmesinde kullanılabileceği sonucuna varılmıştır.

KEY WORDS   *Scymnus subvillosus*, development, fecundity, life table

Coccinellids of the genus *Scymnus* (Coleoptera: Coccinellidae) have been studied as biological control agents in many countries; for example, Egypt (Abdel-Moniem and El-Wahab 2006), Cameroon (Woin et al. 2006), Puerto Rico (Pluke et al. 2005), Japan (Kaneko 2004), China (Liu et al. 2004), Sweden (Wanntorp 2004), and Argentina (Zamar and Claps 2003). *Scymnus ningshanensis* Yu & Tao was introduced from China to the United States for biological control of the hemlock woolly adelgid, *Adelges tsugae* Annand (Butin et al. 2003, 2004). In Turkey, the lady beetle *Scymnus subvillosus* (Goeze) is a widespread aphidophagous predator. It is common in agroecosystems, including stone fruits (especially in apricot [*Prunus* spp.] orchards), apple (*Malus* spp.), and poplar (*Poplus* spp.) trees (Atlıhan et al. 1999, Atlıhan and Kaydan 2002). In particular, it is one of the most abundant predator species in ecosystems where the mealy plum aphid, *Hyalopterus pruni* (Homoptera: Aphididae), is a major pest (Atlıhan et al. 1999).

Proper installation of a natural enemy in pest control requires a comprehensive understanding of its survivorship, development, and reproduction under different environmental factors based on life tables.

[1] Faculty of Agriculture, Plant Protection Department, Yuzuncu Yil University, 65080 Van, Turkey.

[2] Corresponding author: Laboratory of Theoretical Ecology, Department of Entomology, National Chung Hsing University, Taichung, Taiwan, Republic of China (e-mail: hsinchi@dragon.nchu.edu.tw).

Traditional age-specific female life tables (Lewis 1942, Leslie 1945, Birch 1948, Carey 1993) deal with only the female population and ignore the variable developmental rates of individuals. Chi and Liu (1985) developed an age-stage, two-sex life table to include the male population, and the stage differentiation due to variable development occurring among individuals. Chi (1988) gave a detailed description on the data analysis in two-sex life tables. To take the predation by the male population and the stage-specific predation rate into consideration, Chi and Yang (2003), Yu et al. (2005), and Chi and Su (2006) incorporated life tables of predators and parasitoids into studies of predator–prey relationships. To obtain basic information on the biological potential and life table parameters of *S. subvillosus*, we studied the development, survivorship, and reproduction at different temperatures based on the age-stage, two-sex life table.

Materials and Methods

Insect Rearing. *S. subvillosus* were originally collected from apricot trees growing in the experimental orchard of the Agriculture Faculty of Yuzuncu Yil University; subsequently, they were obtained from a laboratory colony that was reared on common reed, *Phragmites australis* (Cavanilles), infested with the mealy plum aphid as prey. The monthly mean temperature at Van was >10°C from May to October, with a peak of mean temperature of 22–25°C in July. Both stock cultures of predator and prey were maintained at a temperature of 25 ± 2°C, 65 ± 5% RH, and a photoperiod of 16:8 (L:D) h, with artificial light of 4,000 lux in a controlled environment room.

Life Table Study. The experiments were conducted in growth chambers at four constant temperatures ranging from 20 to 35 ± 1°C in 5°C increments, 60 ± 10% RH, and a photoperiod of 16:8 (L:D) h, with artificial light (5,000 lux). Eggs of *S. subvillosus* laid within a 24-h period were randomly selected from stock culture, transferred to petri dishes, and provided with an excess of mealy plum aphid as the food source. Developmental and survival data were recorded daily. After adult emergence, females and males were paired and each pair transferred to another petri dish with excessive prey. Survival and fecundity data were recorded daily until the death of each individual. The raw life history data at 25°C were analyzed by Atlıhan and Kaydan (2002) by using the traditional female age-specific life table. The raw data were reanalyzed in this study by using the age-stage, two-sex life table to contrast the results obtained using the female age-specific life table with those from the age-stage, two-sex life table.

Statistical Analyses. When the developmental rate increased linearly with the increase of temperature, we fit the developmental rate to the equation $y = a + bx$ by using linear regression (Sokal and Rohlf 1995), where y is the developmental rate (1/d) and x is the temperature. The thermal summation (K) was then calculated as $K = 1/b$. The developmental threshold (T_0) was calculated as $T_0 = -Ka$. When the develop-

Table 1. Means, standard errors, and sample size (in parentheses) of developmental time of *S. subvillosus* reared on *H. pruni* at four constant temperatures

Temp (°C)	Duration of developmental stages (d)			
	Egg	Larva	Pupa	Total preadult
20	6.2 ± 0.2 (34)	9.5 ± 0.2 (27)	6.9 ± 0.3 (27)	22.6 ± 0.4 (27)
25	4.6 ± 0.6 (30)	6.9 ± 0.2 (25)	5.6 ± 0.2 (25)	17.1 ± 0.4 (25)
30	3.2 ± 0.2 (34)	5.6 ± 0.2 (27)	4.6 ± 0.2 (27)	13.4 ± 0.3 (27)
35	2.9 ± 0.1 (24)	4.8 ± 0.1 (24)	3.1 ± 0.1 (22)	10.6 ± 0.2 (22)

mental rate increased nonlinearly, we fit the data by trying various curvilinear regressions, and the developmental threshold and the thermal summation were not estimated.

The raw data obtained at different temperatures were analyzed according to the age-stage, two-sex life table (Chi and Liu 1985, Chi 1988). The standard errors of the life table parameters were estimated by using the jackknife technique (Meyer et al. 1986, Sokal and Rohlf 1995). The computer program TWOSEX-MSChart (Chi 2005) was used to analyze the life history raw data. The program is written in Visual BASIC for the Windows operating system and is available at http://140.120.197.173/Ecology/prod02.htm (Chung Hsing University, Taichung, Taiwan, Republic of China) and at http://nhsbig.inhs.uiuc.edu/wes/chi.html (Illinois Natural History Survey, Champaign-Urbana, IL). The age-stage specific survival rates (s_{xj}) (where x is the age and j is the stage), age-stage specific fecundity (f_{xj}), age-specific survival rates (l_x), age-specific fecundity (m_x), and population parameters $(r,$ intrinsic rate of increase; $\lambda,$ finite rate of increase; $R_0,$ net reproductive rate; and $T,$ the mean generation time) were calculated. The intrinsic rate of increase is estimated by using iterative bisection method from $\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1$ with age indexed from 0 (Goodman 1982). The mean generation time is defined as the length of time that a population needs to increase to R_0-fold of its size (i.e., $e^{rt} = R_0$ or $\lambda^T = R_0$) at the stable age-stage distribution. The mean generation time is calculated as $T = \ln R_0/r$. The gross reproductive rate (GRR) is calculated as Σm_x. The age-stage life expectancy is calculated according to Chi and Su (2006).

Results

The total developmental time from egg hatching to adult eclosion ranged from 22.6 d at 20°C to 10.6 d at 35°C (Table 1). Like most ectothermic organisms, the developmental time of *S. subvillosus* decreased at higher temperatures (Table 1), and the developmental rate increased with the temperature (Fig. 1). The developmental rates of eggs at different temperatures fit the linear equation $y = -0.0961 + 0.0129x$ with a coefficient of determination (R^2) of 0.969. The linear regression equation for larvae was $y = -0.0281 + 0.00686 x$, $R^2 = 0.997$. The developmental rates of the total preadult stages fit the linear equation $y = -0.0236 + 0.00333x$ $(R^2 = 0.995)$. The thermal sum-
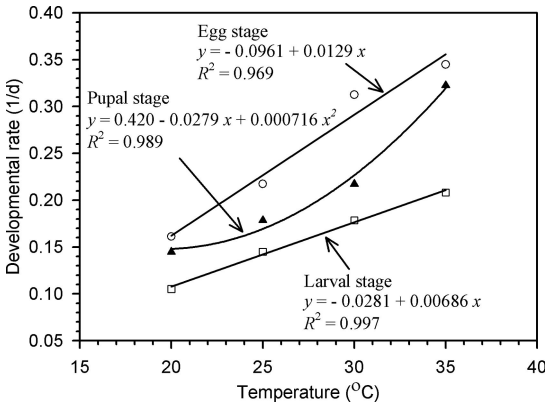
Fig. 1. Developmental rates of egg stage, larval stage, and pupal stage of *S. subvillosus* at four constant temperatures.

mation of the egg stage, the larval stage, and the total preadult stage was 77.5, 145.8 and 300 DD, respectively. The developmental threshold of the egg stage, the larval stage, and the total preadult stages was 7.4, 4.1, and 7.1°C, respectively. Among all preadult stages, the development of pupae was accelerated at higher temperature in comparison to other stages, and the developmental rate can be described by a quadratic equation $y = 0.420 - 0.0279x + 0.000716x^2$ ($R^2 = 0.989$).

The age-stage specific survival rate (s_{xj}) of *S. subvillosus* gives the probability that a newborn will survive to age x and stage j (Fig. 2). The variable developmental rate among individuals results in overlapping among these curves. The probability that a newly laid egg will survive to the adult stage was similar for 20, 25, and 30°C (0.304, 0.350, and 0.312 for females; 0.283, 0.275, and 0.250 for males, respectively), and it was considerably higher than those individuals kept at 35°C (0.12 for females, 0.10 for males). Both females and males kept at 20°C survived longer than those kept at other temperatures. The corresponding preadult mortality was 41.3, 37.5, 43.8, and 78.0% at 20, 25, 30, and 35°C, respectively (Table
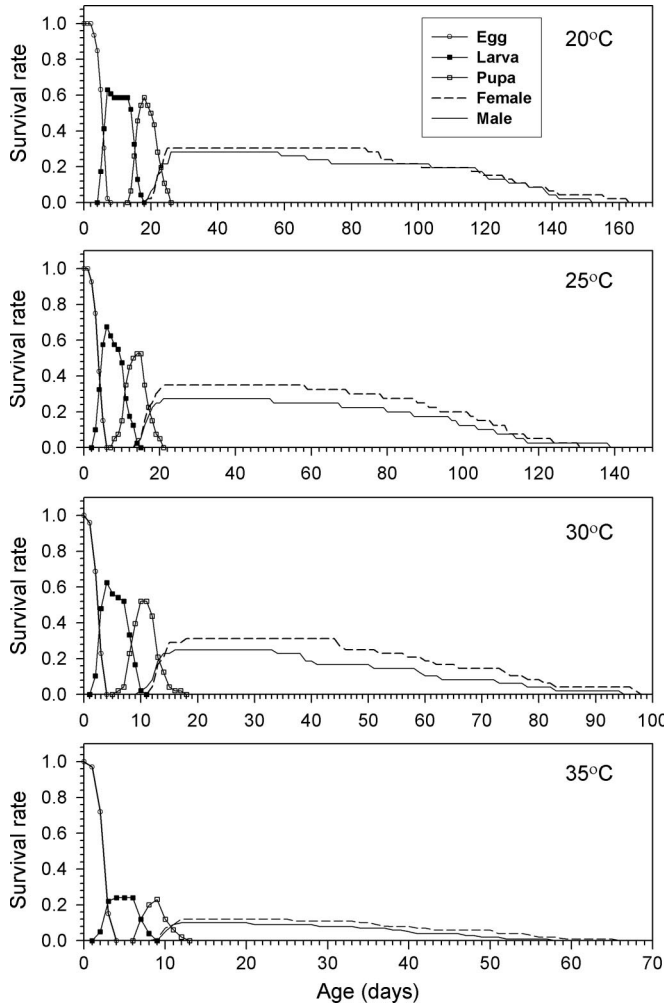

Fig. 2. Age-stage survival rate (s_{xj}) of *S. subvillosus* reared on *H. pruni* at four constant temperatures.

Table 2. Means, standard errors, and sample size (in parentheses) of adult preoviposition period (APOP), total preoviposition period (TPOP), oviposition period, adult longevity, fecundity, and preadult mortality of *S. subvillosus* reared on *H. pruni* at four constant temperatures

Temp (°C)	Preadult mortality (%)	APOP	TPOP	Fecundity (eggs/female)	Adult longevity (d)	
					Female	Male
20	41.3 (46)	9.5 ± 0.6 (14)	32.2 ± 0.7 (14)	216.6 ± 25.5 (14)	97.3 ± 6.7 (14)	92.4 ± 8.4 (13)
25	37.5 (40)	7.4 ± 0.2 (14)	24.6 ± 0.5 (14)	224.8 ± 27.1 (14)	82.1 ± 5.7 (14)	79.8 ± 7.4 (11)
30	43.8 (48)	4.7 ± 0.3 (15)	18.6 ± 0.5 (15)	200.4 ± 22.2 (15)	54.1 ± 4.6 (15)	46.8 ± 5.7 (12)
35	78.0 (100)	4.1 ± 0.4 (12)	14.7 ± 0.5 (12)	39.5 ± 8.6 (12)	35.7 ± 3.4 (12)	30.3 ± 3.6 (10)

2). The length of adult preoviposition period (APOP), total preoviposition period (TPOP), and longevity of the predator were all shortened with an increase of temperature (Table 2). The longest APOP, TPOP, and longevity were obtained at 20°C and the shortest at 35°C. At different temperatures, the mean fecundity per female ranged from 39.5 to 224.8 eggs (Table 2). The mean number of offspring produced by individual *S. subvillosus* of age x and stage j per day is shown with

the age-stage fecundity (f_{xj}) in Fig. 3. Because only females produce offspring, there is only a single curve f_{x4} (i.e., the female is the fourth life stage). Higher peaks of f_{xj}, m_x (the age-specific fecundity) and $l_x m_x$ (age-specific maternity) were observed at 25 and 30°C (Fig. 3).

Population parameters for *S. subvillosus* are presented in Table 3. The intrinsic rate of increase (r) of this coccinellids was the highest at 30°C (0.1395 d^{-1})
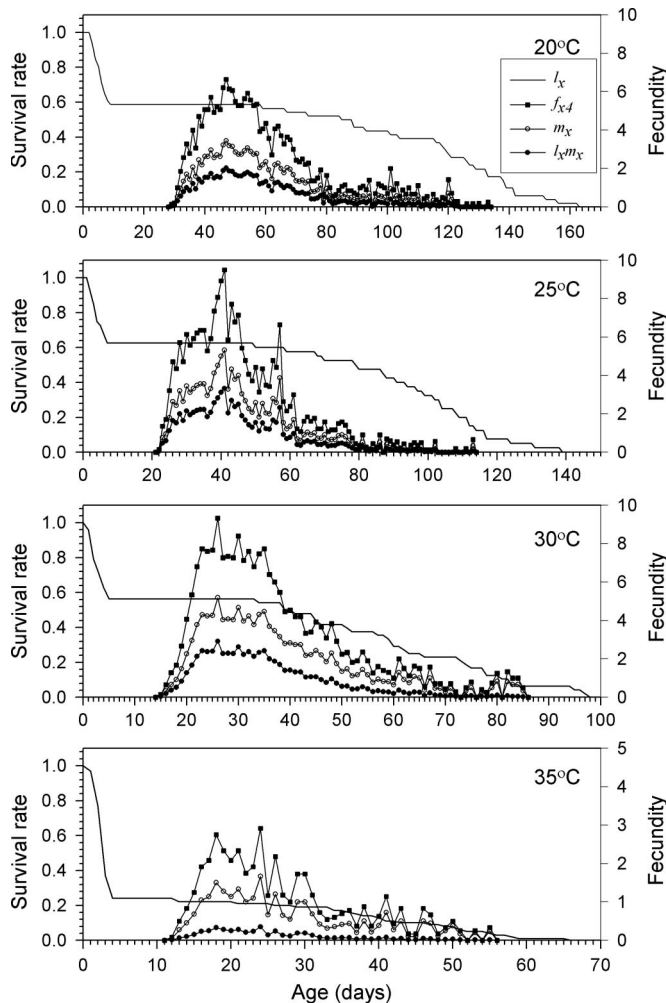

Fig. 3. Age-specific survival rate (l_x), female age specific fecundity (f_{x4}), age-specific fecundity (m_x) and age-specific maternity ($l_x m_x$) of *S. subvillosus* reared on *H. pruni* at four constant temperatures.

Table 3. Population parameters (*r*, intrinsic rate of increase [d^{-1}]; λ, finite rate of increase [d^{-1}]; R_0, net reproductive rate [offspring/individual]; *T*, mean generation time [d]; and GRR, gross reproductive rate [offspring/individual]) of *S. subvillosus* reared on *H. pruni* at four constant temperatures

Temp (°C)	*r*	λ	R_0	*T*	GRR
20	0.0845 ± 0.0060	1.0882 ± 0.0066	65.9 ± 16.7	49.9 ± 1.3	119.3 ± 26.1
25	0.1138 ± 0.0075	1.1205 ± 0.0084	78.7 ± 19.5	38.6 ± 1.1	130.9 ± 28.3
30	0.1395 ± 0.0092	1.1497 ± 0.0105	62.6 ± 15.2	29.9 ± 0.9	129.6 ± 27.5
35	0.0668 ± 0.0181	1.0689 ± 0.0192	4.7 ± 1.6	23.9 ± 2.2	25.6 ± 7.6

and the lowest at 35°C (0.0668 d^{-1}). Because λ = e^r, the finite rate of increase showed a trend similar to *r*. Increasing temperature shortened the mean generation time (*T*) of *S. subvillosus.* The mean generation time was 49.9 d at 20°C, and declined to 23.9 d at 35°C. The net reproduction rate (R_0) was 4.7 offspring per individual at 35°C, and it was considerably lower than the rates obtained at other temperatures. The highest net reproductive rate was obtained at 25°C (R_0 = 78.7 offspring), and values obtained at 20 and 30°C were

comparable to each other. The *GRR* values obtained at 20, 25, and 30°C were similar, and they are considerably higher than those obtained at 35°C. Although the highest net reproductive rate was observed at 25°C, the intrinsic rate of increase and finite rate of increase at 30°C are higher than that at 20 and 25°C due to the fast development and the earlier reproduction at 30°C.

The age-stage specific life expectancy (e_{xj}) of *S. subvillosus* at different temperatures is plotted in Fig. 4. The life expectancy gives the time that an individual
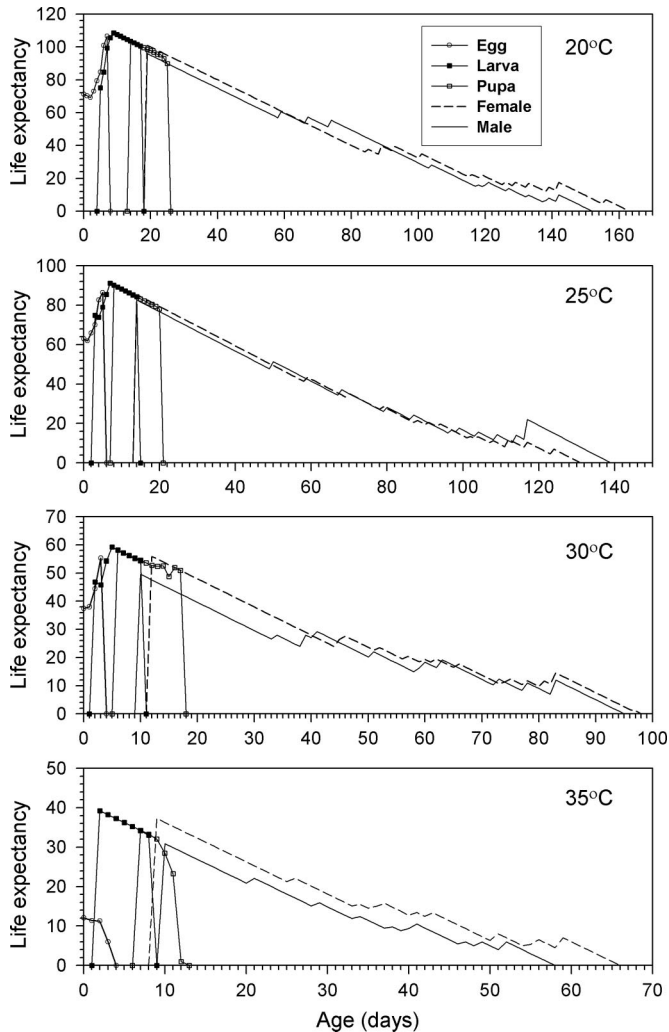

Fig. 4. Age-stage specific life expectancy (e_{xj}) of *S. subvillosus* reared on *H. pruni* at four constant temperatures.
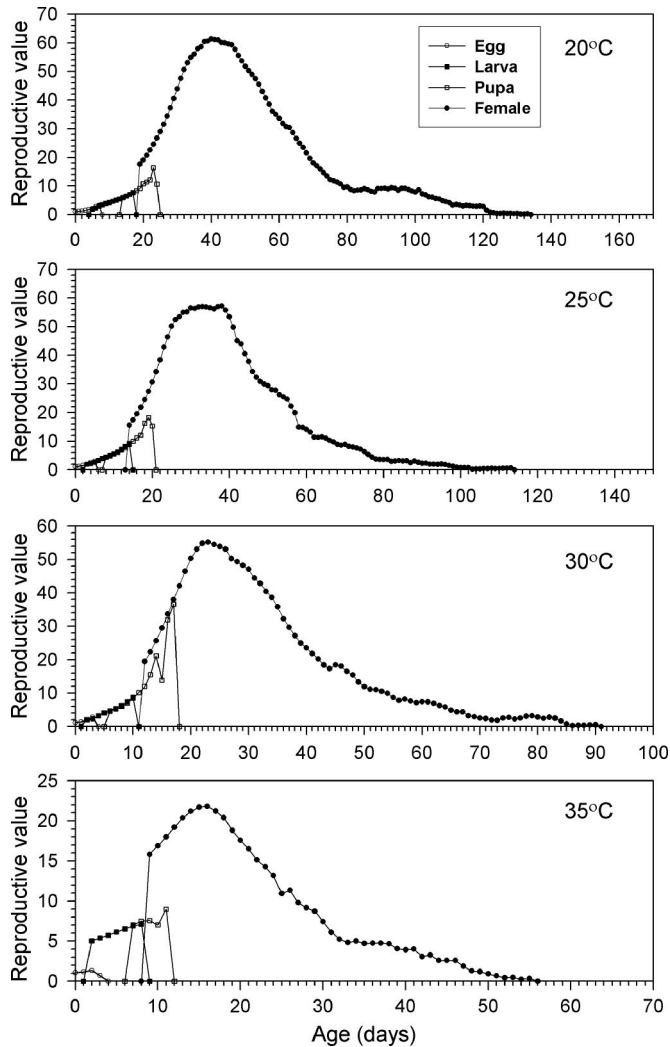
Fig. 5. Age-stage specific reproductive value (v_{xj}) of *S. subvillosus* reared on *H. pruni* at four constant temperatures.

of age x and stage j is expected to live. Because this study was conducted in the laboratory without the adverse effects of field conditions, the life expectancy decreased gradually with aging.

Fisher (1930) defined the reproductive value as the contribution of an individual to the future population. The age-stage reproductive value (v_{xj}) of *S. subvillosus* (Fig. 5) describes the contribution of an individual of age x and stage j to the future population.

Discussion

Our results show that *S. subvillosus* was sensitive to changes in temperature, affecting its developmental time, survival, and fecundity. Shorter immature developmental time at higher temperature might be due to the increasing metabolism in *S. subvillosus.* According to our results, the reproductive rate of *S. subvillosus* was found to be similar to that of several other

members of the genus *Scymnus* feeding on aphids (Hagen 1962). Because the species is multivoltine and it would probably be capable of completing several generations a year in the Van area of Turkey between spring and fall, when prey are readily available. Compared with other *Symnus* species, *S. subvillosus* has a lower developmental threshold (from egg to adult). For instance, the developmental threshold for the total immature stages has been reported as 11.7°C for *S. frontalis* (Naranjo et al. 1990) and 11.1°C for *S. levaillanti* (Uygun and Athhan 2000). Our results were lower than those of the other *Scymnus* species mentioned above. Because many aphid species are tolerant of low temperatures and often emerge in early spring, a lower developmental threshold may be beneficial to *S. subvillosus* in suppressing its prey population. Brown et al. (2003) reported that the total developmental time of *S. louisianae* from egg to adult was 20 d at 23 ± 2°C and that 70% of immatures survived to

adult stage. In their report, however, the daily fecundity curve was constructed based on adult age. Because the developmental rate varies among individuals, ignoring this fact may result in errors in the fecundity and survival curves, and, consequently, in the life table parameters (Chi and Su 2006).

Santha Kumar and Chakraborty (1997) reported that the longevity of female and male *S. nubilus* Mulsant was 57.23 and 49.9 d (at 25–28°C and 65–70% RH), respectively. In our study, the longevity of female and male *S. subvillosus* was 54.1 and 46.8 d at 30°C, respectively. In both species, females lived longer than males. The longevity of females decreased with increasing temperature. These findings are consistent with results observed in other coccinellids (Naranjo et al. 1990; Uygun and Atlıhan 2000, Atlıhan and Özgökçe 2002).

Because both the female fecundity (F) and the net reproductive rate (R_0) are calculated based on the daily fecundity, it is intuitive to believe there are certain relationships between F and R_0. However, the numerous errors in published papers indicated such intuition needs a scientific proof. Chi and Su (2006) mathematically proved that the relationship between F and R_0 is $R_0 = s_a \cdot w \cdot F$ for the female age-specific life table, where w is the female proportion in offspring and s_a is the preadult survival rate. In Uygun and Atlıhan (2000), the preadult survival rate, the female fecundity, the female proportion, and the net reproductive rate of *S. levaillanti* at 30°C was 0.719, 393.1, 0.581, and 141.98, respectively. Their results are inconsistent with the proven relationship between R_0 and F. Persad and Khan (2002) reported the intrinsic rate, the net reproductive rate and the mean generation time for *S. coccivora* as 0.1559 d^{-1}, 220.02 offspring, and 35.6 d, respectively. In their report, the developmental success from egg to adult was 51%. However, the survival curve (l_x) (fig. 4 in Persad and Khan 2002) at adult stage was obviously <30%. These discrepancies are possibly due to the problems resulted from applying the female age-specific life table to an age-stage, two-sex population (Chi and Yang 2003, Yu et al. 2005, Chi and Su 2006). For a two-sex life table, the relationship between the net reproduction rate R_0 and the mean female fecundity F was proven by Chi (1988)) as follows:

$$R_0 = F \cdot (N_f/N) \qquad [1]$$

where N is the total number of eggs used for the life table study at the beginning and N_f is the number of female adults emerged. Yu et al. (2005) proved the relationship among the *GRR*, R_0, and the preadult survivorship (l_a) as follows:

$$GRR > l_a \cdot GRR > R_0 \qquad [2]$$

All of our results for *S. subvillosus* at different temperatures are consistent with relationships of equations 1 and 2. Because *GRR* ignores the different weight of m_x of different age, it should be interpreted with caution (Yu et al. 2005).

In this study, the greater intrinsic rate of increase (r) and finite rate of increase (λ) at 30°C were due to faster immature developmental time, higher daily rate of progeny production and earlier peak in reproduction. The lowest values of life table parameters (r, λ, R_0, and *GRR*) were obtained at 35°C, due to higher immature mortality and reduced fecundity.

The reproductive value (v_{xj}) represents the contribution of an individual of age x and stage j to the future population. The reproductive value of a newborn (v_{01}) is exactly the finite rate of increase (Fig. 5). The reproductive value significantly increases when female adults emerge. For example, because female adults emerged at ages 19, 14, 12, and 9 d at 20, 25, 30, and 35°C, respectively (Fig. 2), the corresponding reproductive values increased to 17.6, 15.5, 19.5, and 15.8 (Fig. 5). However, if old adult females no longer produce offspring, the reproductive value becomes zero. For example, the survival curve of female *S. subvillosus* ended on age 66 d at 35°C (Fig. 2), but the fecundity curve stopped at age 56 d (Fig. 3), yielding reproductive values of zero after age 56 d (Fig. 5). Because the contribution of males to the future population is not defined by Fisher (1930), there is no curve for males.

According to results obtained in this study, temperatures between 25 and 30°C are optimal for population growth of *S. subvillosus.* Uygun and Atlıhan (2000), using a traditional female age-specific life table for *S. levaillanti* (Mulsant), obtained the highest intrinsic rate of 0.151 at 30°C. In our study, the highest intrinsic rate of increase of *S. subvillosus* was 0.1395 at 30°C. Atlıhan and Kaydan (2002) analyzed the raw life history data at 25°C based on the traditional female age-specific life table, and they found that the intrinsic rate of increase, the net reproductive rate, and the mean generation time was 0.110 d^{-1}, 69.9 offspring, and 38.3 d, respectively. Although there are only seemingly minor differences between the population parameters estimated by Atlıhan and Kaydan (2002) and this paper, the age-stage, two-sex life table is capable of giving a comprehensive description of the stage differentiation and stage overlapping (Fig. 2), and it can take both sexes into consideration. Furthermore, the age-stage, two-sex life table gives correct relationship between F and R_0, and it can be used to incorporate the male predation rate in a predator–prey system based on life tables.

Life table study under controlled laboratory conditions reveal the biological potential of the development and fecundity of insect populations. In natural environments, however, most populations are influenced by a variety of changing biotic and abiotic factors. For example, Agarwala et al. (2003) reported that predator fecundity may be affected by both conspecific and heterospecific competitors in a patchy resource. Therefore, results based on laboratory studies should be used with caution. For practical applications, further studies on the efficacy of *S. subvillosus* as a biological control agent and the population growth of both predator and its prey under field conditions are needed to draw firm conclusions. Life tables of *S. subvillosus* obtained at different temperatures are useful bases for the study of population

dynamics, construction of mass rearing programs, and the establishment of management tactics for control of aphid pests. Moreover, because predation rates generally vary with age, stage, and sex (Brown et al. 2003, Chi and Yang 2003, Yu et al. 2005, Chi and Su 2006), an age-stage, two-sex life table provides an important basis for further studies on predator–prey relationships.

Acknowledgments

References Cited

Abdel-Moniem, A.S.H., and T. E. El-Wahab. 2006. Insect pests and predators inhabiting roselle plants, *Hibiscus sabdariffa* L., a medicinal plant in Egypt. Arch. Phytopathol. Plant Prot. 39: 25–32.

Agarwala, B. K., P. Bardhanroy, H. Yasuda, and T. Takizawa. 2003. Effects of conspecific and heterospecific competitors on feeding and oviposition of a predatory ladybird: a laboratory study. Entomol. Exp. Appl. 106: 219–226.

Atlıhan, R., E. Denizhan, and B. Yaşar. 1999. Effects of different preys on development and fecundity of *S. subvillosus* Goeze (Coleoptera: Coccinellidae), pp. 397–406. *In* Proceedings of the 4th Turkish National Congress of Biological Control, 26–29 January 1999, Adana, Turkey. Turkish Entomological Society, Adana, Turkey.

Atlıhan, R., and M. B. Kaydan. 2002. Development, survival and reproduction of three coccinellids feeding on *Hyalopterus pruni* (Geoffer) (Homoptera: Aphididae). Turk. J. Agric. For. 26: 119–124.

Atlıhan, R., and M. S. Özgökçe. 2002. Development, fecundity and prey consumption of *Exochomus nigromaculatus* feeding on *Hyalopterus pruni.* Phytoparasitica 30: 443–450.

Birch, L. C. 1948. The intrinsic rate of natural increase of an insect population. J. Anim. Ecol. 17: 15–26.

Brown, G. C., M. J. Sharkey, and D. W. Johnson. 2003. Bionomics of *Scymnus* (*Pullus*) *louisianae* J. Chapin (Coleoptera: Coccinellidae) as a predator of the soybean aphid, *Aphis glycines* Matsumura (Homoptera: Aphididae). J. Econ. Entomol. 96: 21–24.

Butin, E., J. Elkinton, N. Havill, and M. Montgomery. 2003. Comparison of numerical response and predation effects of two coccinellid species on hemlock woolly adelgid (Homoptera: Adelgidae). J. Econ. Entomol. 96: 763–767.

Butin, E. E., N. P. Havill, J. S. Elkinton, and M. E. Montgomery. 2004. Feeding preference of three lady beetle predators of the hemlock woolly adelgid (Homoptera: Adelgidae). J. Econ. Entomol. 97: 1635–1641.

Carey, J. R. 1993. Applied demography for biologists. Oxford University Press, New York.

Chi, H. 1988. Life-table analysis incorporating both sexes and variable development rates among individuals. Environ. Entomol. 17: 26–34.

Chi, H. 2005. TWOSEX-MSChart: computer program for age-stage, two-sex life table analysis. National Chung Hsing University, Taichung, Taiwan. (http://140.120.197.173/Ecology/prod02.htm).

Chi, H., and H. Liu. 1985. Two new methods for the study of insect population ecology. Acad. Sin. Bull. Inst. Zool. 24: 225–240.

Chi, H., and H. Y. Su. 2006. Age-stage, two-sex life tables of *Aphidius gifuensis* (Ashmead) (Hymenoptera: Braconidae) and its host *Myzus persicae* (Sulzer) (Homoptera: Aphididae) with mathematical proof of the relationship between female fecundity and the net reproductive rate. Environ. Entomol. 35: 10–21.

Chi, H., and T. C. Yang. 2003. Two-sex life table and predation rate of *Propylaea japonica* Thunberg (Coleoptera: Coccinellidae) fed on *Myzus persicae* (Sulzer) (Homoptera: Aphididae). Environ. Entomol. 32: 327–333.

Fisher, R. A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford, United Kingdom.

Goodman, D. 1982. Optimal life histories, optimal notation, and the value of reproductive value. Am. Nat. 119: 803–823.

Hagen, K. S. 1962. Biology and ecology of predaceous Coccinellidae. Annu. Rev. Entomol. 7: 289–326.

Kaneko, S. 2004. Positive impacts of aphid-attending ants on the number of emerging adults of aphid primary parasitoids and hyperparasitoids through exclusion of intraguild predators. Jpn. J. Entomol. (New Ser.). 7: 173–193.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33: 183–212.

Lewis, E. G. 1942. On the generation and growth of a population. Sankhya 6: 93–96.

Liu, J., K. Wu, K. R. Hopper, and K. Zhao. 2004. Population dynamics of *Aphis glycines* (Homoptera: Aphididae) and its natural enemies in soybean in northern China. Ann. Entomol. Soc. Am. 97: 235–239.

Meyer, J. S., C. G. Ingersoll, L. L. McDonald, and M. S. Boyce. 1986. Estimating uncertainty in population growth rates: jackknife vs. bootstrap techniques. Ecology 67: 1156–1166.

Naranjo, S. E., L. G. Robertha, and D. D. Walgenbach. 1990. Development, survival and reproduction of *Scymnus frontalis* (Col.: Coccinellidae), an imported predator of Russian wheat aphid, at four fluctuating temperatures. Ann. Entomol. Soc. Am. 83: 527–531.

Persad, A., and A. Khan. 2002. Comparison of life table parameters for *Maconellicoccus hirsutus, Anagyrus kamali, Cryptolaemus montrouzieri* and *Scymnus coccivora.* BioControl 47: 137–149.

Pluke, R.W.H., A. Escribano, J. P. Michaud, and P. A. Stansly. 2005. Potential impact of lady beetles on *Diaphorina citri* (Homoptera: Psyllidae) in Puerto Rico. Fla. Entomol. 88: 123–128.

Santha Kumar, M. V., and N. Chakraborty. 1997. Biology of *Scymnus nubilus* Mulsant (Coleoptera: Coccinellidae), a native predator of pink mealy bug, *Maconellicoccus hirsutus* (Green) (Hemiptera: Pseudococcidae). J. Entomol. Res. 21: 329–334.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry, 3rd ed. W. H. Freeman, San Francisco, CA.

Uygun, N., and R. Atlıhan. 2000. The effect of temperature on development and fecundity of *Scymnus levaillanti.* BioControl 45: 453–462.

Wanntorp, H. E. 2004. "Musical chairs": the Swedish species of *Scymnus* subg. *Neopullus* (Coleoptera, Coccinellidae) change places. Entomol. Tidskr. 125: 103–109.

Woin, N., C. Volkmar, and T. Ghogomu. 2006. Numerical response of predatory ladybirds (Coccinellidae) to aphid outbreaks and their diversity in major rice ecosystems of Cameroon. Arch. Phytopathol. Plant Prot. 39: 189–196.

Yu, J. Z., H. Chi, and B. H. Chen. 2005. Life table and predation of *Lemnia biplagiata* (Coleoptera: Coccinellidae) fed on *Aphis gossypii* (Homoptera: Aphididae) with a proof on relationship among gross reproduction rate, net reproduction rate and preadult survivorship. Ann. Entomol. Soc. Am. 98: 475–482.

Zamar, M. I., and L. E. Claps. 2003. Morphology of the immature stages and adult of *Pinnaspis aspidistrae* (Hemiptera: Diaspididae) with notes on its biology. Rev. Soc. Entomol. Argent. 62: 35–42.