Influence of temperature on life-table parameters of *Stethorus* gilvifrons (Mulsant) (Coleoptera: Coccinellidae) fed on *Tetrany-* chus urticae Koch

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Keywords

Intrinsic rate of natural increase, ladybird predator, population growth, survivorship, two-spotted spider mite

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Abstract

The influence of temperature on life-table parameters, fecundity and survivorship of the predatory ladybird, Stethorus gilvifrons, fed on Tetranychus urticae was determined at seven constant temperatures of 15°C, 20°C, 25°C, 28°C, 30°C, 35°C and 40°C. No development was observed at 40°C, thus being regarded as the threshold for the development of S. gilvifrons. The results indicate a significant decrease in male and female longevity with increasing temperature from 15°C to 35°C. The longest and shortest longevity were 18.40 and 12.75 days for males and 17.40 and 8.80 days for females, respectively. The intrinsic rate of natural increase (r_m) and the net reproductive rate (R_0) of S. gilvifrons linearly increased with increasing temperatures from 15°C to 35°C, while the mean generation time (T) and doubling time (DT) decreased linearly within this temperature range. The highest values of r_m (0.240 females/ female/day) and R_0 (59.27 females/female) and the lowest mean generation time (17.01 days) and DT (2.88 days) were recorded at 35°C. The maximum (185.50 eggs) and minimum (25.50 eggs) measurement of total fecundity was also recorded at 35°C and 15°C, respectively. The results indicate that temperature greatly affected fecundity, survivorship and life-table parameters of S. gilvifrons, and that 35°C is a suitable temperature for population growth of this predator.

Introduction

The two-spotted spider mite, *Tetranychus urticae* Koch, is one of the most important arthropod pests of agricultural crops and ornamental plants in Iran and many other countries. In recent years, several strategies have been developed to manage *T. urticae* on economically important crops (Bostanian et al. 2003). One of these strategies is to use predatory mites and insects in integrated pest management (IPM) programmes (Roy et al. 2005). Understanding population growth rate, dispersal ability, voracity, fitness and foraging strategies of a predator is of primary importance in the development of successful biological control programmes (Fathipour et al.

2005; van Klinken and Raghu 2006). In developing an effective IPM programme to control pests, it would be advantageous to maximize the effectiveness of several natural enemies (Zhang et al. 2007); however, various biotic and abiotic factors may reduce this effectiveness (Soleyman-Nezhadiyan and Laughlin 1998; Haghani et al. 2007a; Zamani et al. 2007). One of the most important and critical abiotic factors that greatly affect biological characteristics of both pests and their natural enemies is temperature (Haghani et al. 2007a,b). Therefore, effects of temperature on performance and effectiveness of natural enemies need to be evaluated.

Predacious coccinellids are important natural enemies of several small phytophagous insects and mites and are considered as potentially good biocontrol agents (Zhang et al. 2007). All known species of the genus Stethorus are predators of spider mites, and several species have been reported as biocontrol agents of tetranychid pests in agricultural systems (Roy et al. 1999). The predatory ladybird beetle, Stethorus gilvifrons (Mulsant) is a predator preving on different life stages of two-spotted spider mites. However, there are only few papers specifically dealing with either the voracity and or the feeding behaviour of this predator (Hajizadeh et al. 1992; Afshari et al. 2001; Kheradpir et al. 2006). Demographic studies on Stethorus ladybirds deal with other species of this genus. Roy et al. (2002, 2003) studied the effects of temperature on development and intrinsic rates of natural increase (r_m) of Stethorus punctillum (Weise) on its spider mite prey, and Mori et al. (2005) investigated the effect of temperature on life history of Stethorus japonicus Kamiya.

The intrinsic rate of natural increase (r_m) is a key demographic parameter in the prediction of population growth potential under given environmental conditions (Andrewartha and Birch 1954). Although the use of r_m has been criticized for its assumption of a stable age distribution in the populations studied, it has been demonstrated to be both a predictive and comparative measure of population growth potential (Hulting et al. 1990). A number of factors have been shown to affect r_m and related demographic parameters. In arthropods, temperature is known to be a key factor in this regard (Medeiros et al. 2003). Development, longevity, fecundity, fertility and other life-history parameters of arthropods are highly correlated with temperature (Birch 1948). More specifically, life tables facilitate the understanding of insect population dynamics (Wittmeyer and Coudron 2001). The cohort life table gives the most comprehensive description of the survivorship, development and reproduction of a population which are fundamental factors in both theoretical and applied population ecology (Chi and Yang 2003).

In the present study, the effects of temperature on survival, fecundity and life-table parameters of *S. gil-vifrons* were determined in order to assess the suitability of this predator for use in biological control programmes against spider mites. The most important rationale in this study, however, was to find a suitable temperature regime resulting in high fitness and proper mass rearing of *S. gilvifrons* fed on *T. urticae*.

25°C, 60-70% relative humidity and a photoperiod of 16L:8D h. Ladybirds were reared on bean leaves containing spider mites placed in Plexiglas cages $(10 \text{ cm} \times 15 \text{ cm} \times 20 \text{ cm})$ under the same laboratory conditions. Water was provided for the insects and also used to keep the leaves fresh using a moistened dental wick at the end of the petioles. Seedlings of P. vulgaris were grown in pots to three to four leaf stage with a mixture of sand, clay and peat moss. The eggs on leaf discs (inside Petri dishes with 6 cm diameter) were placed in growth chambers programmed for seven constant temperature regimes of 15°C, 20°C, 25°C, 28°C, 30°C, 35°C and 40°C, relative humidity of 60-70% and a photoperiod of 16L:8D h. The emerging larvae were also established on leaf discs containing immature stages of T. urticae. The leaf discs were placed on a moistened sponge to keep them fresh and every 2 or 3 days, the leaf discs were replaced with new ones.

The spider mites and the ladybird predators used in

this study were originally collected from bean fields in the vicinity of Tehran, Iran in 2005. The spider

mite individuals were reared on bean leaves (Phase-

olous vulgaris L. cv. Sunray) in growth chambers at

Survival and longevity

Materials and Methods

Experimental conditions

To obtain synchronized eggs, ladybird females were incubated at 25°C on bean leaf discs. Newly laid eggs of S. gilvifrons were then placed individually on the leaf discs. Upon hatching S. gilvifrons larvae were fed daily with immature stages of T. urticae in excess. Immature predators were transferred to fresh leaf discs every 2 or 3 days until they are matured. After maturing, a female was placed with a male (replication numbers depending on the number of matured insects at different temperatures) in cages and they were allowed to reproduce. The predator eggs were counted and removed daily and the dead males were replaced. Longevity (from adult emergence to adult death) of both male and female insects at all the seven temperatures was determined. Age-specific survival rates or survivorship (l_x) and life expectancy (e_x) of all stages of the predator were recorded every day for each experimental temperature according to Carey (1993).

Life-table parameters

Life-table parameters were calculated using the immature and adult predators' survival rate and agespecific fecundity (m_x) based on the females reared at the seven constant temperatures. The following demographic parameters were calculated: net reproductive rate (R_0) , intrinsic rate of natural increase (r_m) , finite rate of increase (λ) , mean generation time (T) and doubling time (DT) (Carey 1993). The total and daily fecundity of *S. gilvifrons* were also determined and statistically compared at different temperatures.

Statistical analysis

The effect of temperature on adult longevity was analysed using one-way ANOVA. If significant differences were detected, multiple comparisons were made using the LSD procedure (P < 0.05). Differences in R_0 , r_m , λ , T, and DT values were tested for significance by estimating variances through the jackknife procedure (Meyer et al. 1986; Maia et al. 2000). The jackknife procedure was also used to estimate variance for r_m and other life-table parameters. This procedure is mostly used to estimate the variance between and bias of estimators. Algorithms for the jackknife estimation of the means and variances are described only for R_0 , but similar procedures were used for the other parameters (r_m , λ , T and DT). The steps for the application of the method are as follows:

(a) Estimation of R_0 , r_m , λ , T, and DT using the survival and fecundity data from all n number of females, referred to as the true calculation. At this point, called step zero, the estimates obtained are denoted as $R_{0(\text{all})}$, $r_{m(\text{all})}$, $\lambda_{(\text{all})}$, $T_{(\text{all})}$, and DT_(all).

(b) The procedure described in part (a) is repeated for n times, each time excluding a different female. In so doing, in each step *i*, data of n - 1 females are taken to estimate the parameters for each step, now named $R_{0(i)}$, $r_{m(i)}$, $\lambda_{(i)}$, $T_{(i)}$, and $DT_{(i)}$.

(c) In each step *i*, pseudo values are calculated for each parameter, subtracting the estimate in step zero from the estimate in step *i*. For instance, the pseudo values of R_0 [$R_{0(j)}$] were calculated for the n samples using the following equation:

$$R_{0(i)} = n \times R_{0(\text{all})} - (n-1) \times R_{0(i)}$$
(1)

(d) After calculating all n number of pseudo-values for R_0 , jackknife estimates of the mean $[R_{0(mean)}]$,

variance $[VARR_{0(mean)}]$, and standard error $[SER_{0(mean)}]$ were calculated by the following equations:

$$R_{0(\text{mean})} = \frac{\sum_{j=1}^{n} R_{0(j)}}{n}$$
(2)

$$VARR_{0(mean)} = \frac{\sum_{j=1}^{n} (R_{0(j)} - R_{0(all)})^2}{n-1}$$
(3)

$$SER_{0(mean)} = \sqrt{\frac{VARR_{0(mean)}}{n}}$$
 (4)

The mean values of (n - 1) jackknife pseudo values for each temperature were subjected to an ANOVA (Zamani et al. 2006).

Results

Male and female longevity

Stethorus gilvifrons has eight life stages, i.e., egg, 1st, 2nd, 3rd and 4th instar larvae, pre-pupa, pupa and adult. This predator successfully developed to adulthood at temperatures from 15°C to 35°C. At 40°C, no development was observed. The rates of male and female longevity are shown in table 1. The longevity of females at 15°C was significantly higher than that at other temperatures tested. At 15°C and 35°C, male longevity was 18.40 and 12.75 days and female longevity was 17.40 and 8.80 days, respectively (table 1). Temperature had a significant effect on the longevity of both sexes of S. gilvifrons. The comparison of longevity between male and female insects at each temperature indicated a significant difference only at 35° C (P < 0.01). The results suggest that temperature affects the adult longevity of S. gilvifrons and the effects on male and females were very similar.

Survival, fecundity and life expectancy

The eggs failed to hatch at 40°C and therefore the survival rate at this temperature was zero. Age-specific survivorship data of *S. gilvifrons* reared at the other six constant temperatures are presented in fig. 1. Higher temperatures caused a steeper decline in survivorship, with the longest survival at 15°C, and highest mortality rates at 30°C and 35°C, respectively. At temperatures of 15°C, 20°C, 25°C, 28°C, 30°C and 35°C, the last female of the tested cohorts died at the age of 75, 50, 38, 36, 29, and

Table 1 Male and female longevity (mean \pm SE) of S. gilvifrons at six constant temperatures on T. urticae

Longevity	15°C	20°C	25°C	28°C	30°C	35°C***
Male** Female	18.40 ± 2.42 a* 17.40 ±1.44 a	16.00 ± 0.80 ab 15.00 ± 0.71 b	17.75 ± 0.76 a 15.33 \pm 1.21 b	16.33 ± 1.21 ab 14.50 \pm 0.46 b	14.00 ± 1.21 bc 11.40 \pm 1.10 c	$\begin{array}{c} 12.75\pm1.20~\text{c} \\ 8.80\pm1.03~\text{d} \end{array}$

*The means followed by different letters within a same row are significantly different (P < 0.01; LSD).

In comparison of longevity between male and female insects in each temperature, there was only significant difference at 35°C (P < 0.01). *There was no development at 40°C.

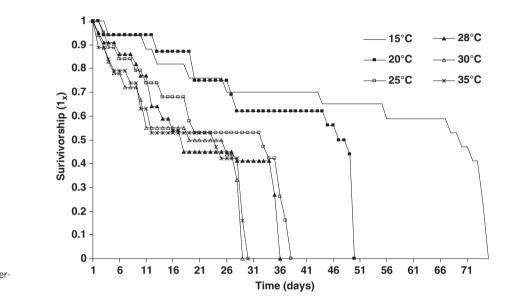


Fig. 1 Survivorship curves of S. gilvifrons at six constant temperatures on T. urticae.

30 days, respectively. Survivorship curves were similar at 25°C and 28°C and also at 30°C and 35°C. Temperature had a great effect on age-specific fecundity (m_x : female progeny per female per day) (fig. 2) and total and daily fecundity (table 2) of S. gilvifrons. The age-specific fecundity increased with increasing temperatures between 15°C and 35°C. In this range, the age at first oviposition was 54, 34, 22, 20, 16 and 13 days and at last oviposition was 67, 47, 34, 34, 30 and 27 days (fig. 2). The results indicated that the duration of the period of oviposition was similar at all temperatures (12–14 days). The total and daily fecundity (number of eggs produced per female during the oviposition period and per day, respectively) were significantly affected by temperature, both being higher when temperature increased from 15°C to 35°C; although between 28°C and 30°C, no significant differences were observed (table 2). Life expectancy of S. gilvifrons at six constant temperatures is presented in fig. 3. The life expectancy (e_x) of S. gilvifrons from the first day of life at 15-35°C was about 50, 35,

23, 20, 17 and 17 days revealing that the e_x decreased with increasing temperature from 15°C to 35°C. The decreasing life expectancy and life span of the predator with increasing temperature is mainly due to the decrease in time required for development as the temperature rises. The highest life expectancy was observed at 15°C.

Life-table parameters

The effect of temperature on the net reproductive rate (R_0), intrinsic rate of natural increase (r_m), finite rate of increase (λ), mean generation time (T) and DT is presented in table 3. Temperature had a strong effect on net reproductive rate and intrinsic rate of natural increase in the predator. The intrinsic rate of natural increase of *S. gilvifrons* rose with an increase in temperature from 15°C to 35°C. The highest value of r_m was 0.240, observed at 35°C, while the lowest value was recorded at 15°C (0.035). The net reproductive rate was highest at 35°C with 59.27 female offspring per female ladybird. Increasing the

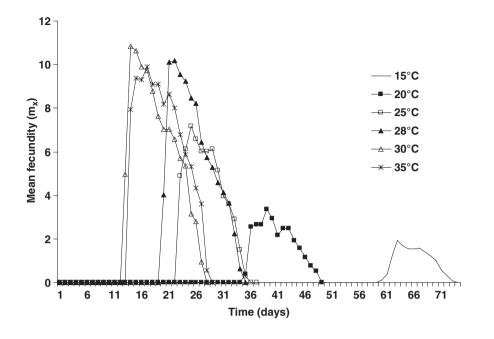


Fig. 2 Age-specific fecundity curves of *S. gilvifrons* at six constant temperatures on *T. urticae*.

Table 2 Total and daily fecundity (mean \pm SE) of S. gilvifrons at six constant temperatures on T. urticae

Fecundity	15°C	20°C	25°C	28°C	30°C	35°C
Total Daily	25.50 ± 2.61 e 2.57 ± 0.16 e	$\begin{array}{c} 47.11 \pm 3.21 \text{ d} \\ 4.14 \pm 0.16 \text{ d} \end{array}$	$\begin{array}{c} 102.50 \pm 8.87 \text{ c} \\ 9.80 \pm 0.69 \text{ c} \end{array}$	145.20 ± 12.12 b 11.88 \pm 0.37 b	150.90 ± 15.28 b 12.44 ± 0.28 b	185.50 ± 14.00 a 14.48 \pm 0.47 a

*The means followed by different letters within a same row are significantly different (P < 0.01; LSD).

**There was no development at 40°C.

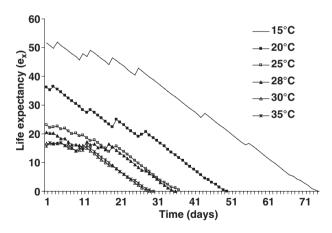


Fig. 3 Life expectancy (e_x) curves of *S. gilvifrons* at six constant temperatures on *T. urticae*.

temperature resulted in a shorter mean generation time (17.01 days at 35° C; 64.33 days at 15° C). The DT was also shortest at 35° C (2.88 days), while the finite rate of increase was highest at this temperature (1.271) (table 3).

Discussion

The results of our experiment on temperaturedependent life-table parameters of S. gilvifrons demonstrated a strong correlation between temperature and male and female longevity (table 1), survivorship (fig. 1), age-specific fecundity (fig. 2), life expectancy (fig. 3), total and daily fecundity (table 2), life-table parameters (table 3) and developmental rate. Our findings indicate that the performance of S. gilvifrons was optimal at higher temperatures of around 35°C, but less than 40°C. The highest value of the most critical demographic parameter, the intrinsic rate of natural increase (r_m) , was observed at 35°C, and a rapid population growth of this predator at or around this temperature could be expected. This parameter is an index of population increase and is intensively used in population growth models and the prediction of population dynamics. A trend towards maximal performance at 35°C and lowest performance at 15°C was also observed with respect to net reproductive rate (R_0) and finite rate of increase (λ) . This

Parameter	15°C	20°C	25°C	28°C	30°C	35°C**
Ro	10.08 ± 1.26 f*	16.38 ± 0.99 e	31.33 ± 1.99 d	39.21 ± 2.59 c	47.54 ± 3.68 b	59.27 ± 3.59 a
r _m	0.035 \pm 0.01 f	$0.072\pm0.01~\text{e}$	0.133 \pm 0.01 d	$0.145\pm0.01~c$	0.191 ± 0.01 b	0.240 ± 0.01 a
λ	$1.036 \pm 0.01 \; f$	$1.075 \pm 0.01 \ e$	$1.142 \pm 0.01 \ d$	$1.156 \pm 0.01 \ { m c}$	$1.211 \pm 0.01 \ b$	1.271 ± 0.01 a
Т	64.33 ± 1.40 a	38.70 ± 1.71 b	25.92 ± 0.33 c	$25.31 \pm 0.50 \ \mathrm{c}$	$20.17\pm0.22~\text{d}$	$17.01 \pm 0.04 \; e$
DT	$19.93 \pm 2.05 \; a$	$9.60\pm0.44~b$	5.21 ± 0.11 c	$4.78\pm0.11~\mathrm{c}$	$3.62\pm0.07~d$	$2.88\pm0.04~\text{e}$

Table 3 Life-table parameters (mean \pm SE) of S. gilvifrons at six constant temperatures on T. urticae

*The means followed by different letters within a same row are significantly different (P < 0.01; LSD).

**There was no development at 40°C.

predator could increase its population at R_0 -fold (T) and 2-fold (DT) in the shortest period of time at 35°C, followed by 30°C, 28°C, 25°C, 20°C and 15°C; while there was no significant difference between 25°C and 28°C (table 3). The r_m value depends on a number of other life-history parameters, one of which is fecundity. The results of this study indicate a higher daily and total fecundity of *S. gilvifrons* at 35°C (table 2) as demonstrated for r_m .

No other studies have previously examined the effect of temperature on life-table parameters of S. gilvifrons, but there are similar studies on other species of ladybirds that calculated demographic parameters, especially r_m , and factors affecting these parameters. In practice, demographic parameters are difficult to compare between studies because of species differences, genetic variation, differences in rearing methods and other experimental conditions. Roy et al. (2003) reviewed the literature and listed the rate of natural increase in 15 species of coccinellids from the genera of Stethorus, Coccinella, Coleomegilla, Olla, Propylea, Diomus, Exochomus, Hyperaspis and Rodalia specializing on different prev taxa (acariphagous, aphidophagous and coccidophagous) as measured at a temperature close to 25°C. A comparison of r_m in S. gilvifrons in the current study with that of other acariphagous coccinellids (Stethorus spp.) measured at or around 25°C shows that the intrinsic rate of natural increase of S. gilvifrons (0.133) was greater than that measured for S. punctillum Weise (0.100; Roy et al. 2003) but less than that measured for Stethorus loxtoni Britton et Lee (0.152; Richardson 1977), Stethorus madecassus Chazeau (0.155; Chazeau 1974), Stethorus picipes Casey (0.121; Tanigoshi and McMurtry 1977), Stethorus loi (0.160; Shih et al. 1991) and S. japonicus (0.156; Mori et al. 2005). Roy et al. (2003) reported that the highest r_m of S. punctillum was 0.17 at 30°C, but the highest r_m of S. gilvifrons measured in our study was 0.24 when tested at

35°C. The value of this parameter for *S. gilvifrons* at 30°C was 0.19 which is greater than that measured for *S. punctillum* at the same temperature. This illustrates the higher capacity for population growth of *S. gilvifrons*. The r_m of *S. punctillum* increased almost linearly with temperature in the range 14–34°C to reach a maximum value before rapidly decreasing and displaying an asymmetrical dome-shaped pattern (Roy et al. 2003). In the present study, the rate of r_m for *S. gilvifrons* increased linearly from 15°C to 35°C where it peaked.

The total fecundity at 25°C in S. gilvifrons (102.20 eggs) was less than that measured at or around the same temperature for S. japonicus (500.7 eggs; Mori et al. 2005), S. madecassus (184.3; Chazeau 1974), S. picipes (221.0; Tanigoshi and McMurtry 1977) and S. punctillum (279.5; Roy et al. 2003), suggesting that S. gilvifrons has lower total fecundity at this temperature in comparison with these other species. The net reproductive rate of S. gilvifrons at 25°C (31.33 females/female) was also lower than that measured for the three other Stethorus species of S. japonicus (270.5; Mori et al. 2005), S. madecassus (92.4; Chazeau 1974) and S. picipes (103.3; Tanigoshi and McMurtry 1977). It should be noted that the most appropriate demographic parameter for comparing different species or different conditions is r_m , as this parameter is a product of different biological parameters including fecundity, reproductive rate, immature mortality, sex ratio and developmental rate. However, suitable environmental conditions for rearing and population increase of a given species need to be considered as well. For example, although the fecundity and net reproductive rate of S. gilvifrons is noticeably less than that of S. japonicus (Mori et al. 2005), their rates of natural increase (r_m) under optimum temperatures (35°C for S. gilvifrons and 30°C for S. japonicus) are similar (0.240 and 0.241, respectively).

This work described the temperature-dependent fecundity and population growth parameters of S. gilvifrons under broad range of temperatures generally prevailing in Tehran province, Iran. From the present results, on the capacity of this species to show population growth and from its foraging behaviour, S. gilvifrons is an appropriate biocontrol agent that can be used in the integrated management of spider mites, especially in controlled environments such as greenhouses. Using biological pest control on greenhouse crops, it should be possible to produce the same crops without the need to use conventional pesticides. This would also imply a cleaner environment and satisfy consumer demands for pesticide-free food and sustainable crop protection (van Lenteren 2000). The main reason for the use of biological control in recent years especially on protected crops is the presence of resistance to pesticides among several key pests in greenhouses (van Roermund et al. 1997). The key to use environmental controls in an insect and mite management programme is to know how environmental conditions affect both the pest and their natural enemies. Temperature may strongly affect the relationship between a natural enemy and the target pest (Zamani et al. 2007), and focusing on this abiotic factor in order to demonstrate its main effect on efficiency of natural enemies especially in greenhouses is essential. Relatively, few studies have examined temperature, relative humidity, host plant species and other variable conditions preferences of Stethorus species (e.g. Rott and Ponsonby 2000; Roy et al. 2002; Yoder et al. 2003; Fiaboe et al. 2007), and of these, most of the studies describe only rearing conditions (Putman 1955; Tanigoshi and McMurtry 1977; Houck 1986, 1991) or field situations (Felland and Hull 1996). However, all these publications have emphasized on this crucial subject that variable conditions (e.g. temperature) may affect the efficiency and performance of natural enemies in both greenhouse and outdoor environments, and in order to get desirable results of biological control programmes, we should choose the best physical conditions, especially appropriate temperature range, as an important abiotic factor.

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