TEMPERATURE-DEPENDENT DEVELOPMENT
OF IMMATURE STAGES OF PREDATORY LADYBIRD BEETLE
STETHORUS VAGANS (COLEOPTERA: COCCINELLIDAE)
AT CONSTANT AND FLUCTUATING TEMPERATURES

Inamullah Khan1 and Robert Spooner-Hart2
1Department of Plant Protection, The University of Agriculture Peshawar
Khyber Pakhtunkhwa Pakistan, E-mail: dr.inam@aup.edu.pk
2University of Western Sydney, Hawkesbury Campus, Penrith, NSW 2751, Australia
E-mail: R.Spooner-Hart@westernsydney.edu.au

Influence of temperature on the development of the predatory ladybird, Stethorus vagans Blackburn, fed on Tetranychus urticae Koch was assessed at seven constant (10, 12, 15, 20, 25, 30 and 35 °C) and fluctuating (12.7–32.1 °C) temperatures. There was a strong positive correlation \((r = 0.99)\) between rate of development and temperature. The development times from egg to adult emergence were 65.2±2.3 and 9.2±0.3 days at 12 and 30 °C constant, respectively and 15.4±0.3 days at fluctuating temperature. Average egg incubation period decreased from 16.5±0.8 to 2.18±0.2 days with increasing temperatures from 12 to 30 °C, respectively and was 4.1±0.3 days at the fluctuating temperature. Eggs did not develop at 10 °C; however, they could survive a long period of exposure to this temperature. None of two hundred eggs that were placed at a constant temperature of 10 °C for 60 days hatched; but when they were subsequently exposed to ≥15 °C, more than 120 of them hatched. Eggs appeared to develop normally at 35 °C, however, larvae died before or immediately after emergence. The lower development threshold temperature for egg, 1st, 2nd, 3rd, 4th larval instars, pupal and all these stages combined was 10.1, 9.5, 9.5, 9.1, 8.2, 8.0, and 9.1 °C, respectively. Degree-day (DD) accumulation was also calculated for each stage as well as for all stages combined. It was estimated to be 189.2±4.8 DD at 12 °C and 207.8±6.9 DD at 30 °C constant, respectively, and 189.1±5.0 DD at fluctuating temperatures.

Key words: rate of development, predatory ladybird beetle, Stethorus vagans, Degree Days, two-spotted mite.

INTRODUCTION

Two-spotted spider mite (TSSM), Tetranychus urticae Koch, is a major pest of more than 200 plants of economic importance worldwide, including a large number of greenhouse crops, a wide range of field crops, vegetables, strawberry, deciduous fruit trees, walnuts, almond, berries hops, cucurbits, cut flowers, ornamental shrubs, vines, and various other plants (Costello et al. 1992, Gough 1992, Hutchinson 1992, Bower & Thwaite 1995, McMaugh, 1998, Han et al. 2003, Jung 2005, Kheradpir et al. 2007). A number of acaricides and insecticides have been introduced for the control of T. urticae, but it has

Hungarian Natural History Museum, Budapest
developed resistance against these chemicals, while some were withdrawal due to health hazards and environmental pollution (Penrose et al. 1997). This suggests that the problem of controlling T. urticae deteriorates if the cost of developing and marketing of new compounds becomes prohibitive (Readshaw 1975). Therefore, interest has increased in biological control of this pest. Many insects as well as several families of mites are recorded as good biological agents of tetranychid pests (Gordon & Anderson 1979, Houston 1980, Helle & Sabelis 1985).

All known species of Stethorus have been reported to attack spider mites of economic importance. Both adults and larvae are highly specialized predators of tetranychid mites (Houston 1980, Helle & Sabelis 1985, Hull 1977, Roy et al. 2005). Biological studies have been conducted on several species of Stethorus. Most of the species complete their life cycle (egg-adult) in two weeks and have five generations a year under optimal temperature conditions, which is slightly longer than that required for the development of most mite species in green houses in England and in field in India (Jeppson et al. 1975, Pavlova 1975, Singh & Ray 1977). One of the species belong to this genus, Stethorus vagans Koch (Coleoptera: Coccinellidae), native to Australia, has been observed in close association with T. urticae in various agricultural and horticultural crops, and ornamental plants system (Readshaw 1975, Gordon & Anderson 1979, Houston 1980, Helle & Sabelis 1985). This species is capable of detecting and attacking populations of T. urticae at very low density, distributed in small and widely scattered patches (Khan 2001). However, there are only a few papers published on this species, mainly on its taxonomic description and its presence in the orchards where T. urticae are found (Readshaw 1975, Gordon & Anderson 1979, Houston 1980, Helle & Sabelis 1985).

The success of biological control is dependent on the synchronization of the pest and predator, which depends on their population growth rate, dispersal ability, voracity and fitness. Synchronization both species is mainly dependent on biotic and abiotic factors, of which the latter play a major role (Huffaker et al. 1999). Among abiotic factors temperature, photoperiod and relative humidity are probably the most important that influence the rate of development and survival of living organisms; however temperature is the most crucial one, as it greatly affects developmental rate of various insect pests and their natural enemies, which in turn influence their seasonal occurrence and population dynamics (Andrewartha & Birch 1954, Honek & Kocourk 1990, Huffaker et al. 1999, Roy et al. 2002). Knowledge of temperature-dependent development is essential for understanding the dynamics of predator-prey relationships, their biology, ecology and distribution, which are also useful in the enhancing of mass rearing (Rodriguez-Saona & Miller 1999), and predicting their development and activity in the field (Fan et al. 1992).
Temperature-dependent models are widely used to predict population density and rate of development of insect pests and their natural enemies (Woodson & Edelson 1988, Hayakawa et al. 1990, Deloach 1974), for example corn leaf aphid, Rhopaloniphum maidis (Elliott et al. 1988), navel orange worm Amyelois transitella (Sanderson et al. 1989), Mexican bean beetle Epilachna varivestis (Fan et al. 1992), and the coccinellid Hippodamia sinuata (Michels & Beile 1991) and Stethorus bifidus (Petersons et al. 1994). No data have been published on the Degree-Day (DD) requirement in the genus Stethorus, except for S. bifidus. A study had already been done on the developmental rate and DD of Tetranychus urticae, while, no similar data were available for its predator Stethorus vagans (Coleoptera: Coccinellidae). Therefore the present study was undertaken to obtain developmental data over a wide range of constant and fluctuating temperatures, which could be used to calculate the lower developmental threshold temperatures and to construct a DD model for S. vagans. It also aimed to assist interpretation and prediction of seasonal development of S. vagans in the field and its synchronization with its host T. urticae.

MATERIAL AND METHODS

Field collection and stock colony

Adult predatory ladybird beetle Stethorus vagans were collected from the field on potted French bean plants (Vicia faba cv. Redland Pioneer) infested with Tetranychus urticae. A culture colony from these predators was established at 25±0.1 °C with a photoperiod of 16:8 (L: D) and RH 60±5 % in a temperature-controlled cabinet (Thermoline incubators (internal dimension 122 × 52.5 × 43 cm). Catalogue number RI 250, Thermoline Scientific Equipment Pty Ltd., 40 Blackstone Street, Wetherill Park, NSW 2164, Australia) in the laboratory. Stock colony of TSSM was maintained on French bean plants in a screen house between 25–27 °C and RH 50–75% for regularly supply for the S. vagans culture and experimental work in the laboratory and field. All collections and experimental work were carried out at the Centre for Horticulture and Plant Sciences, University of Western Sydney, Hawkesbury campus, Richmond (33°36′S, 150°44′E), New South Wales, Sydney, Australia.

Experimental conditions

S. vagans development was studied at nine constant (10–40 °C) as well as at fluctuating temperatures (12.7–32.1 °C). Initially, adult predators were randomly selected from the stock colony and paired over a 2.5 cm diameter bean leaf discs infested with TSSM. These discs were maintained on water-saturated foam in polystyrene sealable petri dishes (Falcon plastic, Oxnard, CA), which had a 3-cm diameter hole in the upper lid and was covered with nylon cloth. These petri dishes were randomly allocated to nine Thermoline illuminated incubators units set at constant temperatures, 10, 12, 15, 20, 25, 30, 32, 35 and 40 °C (±0.1 °C) at photoperiod of 16L: 8D h and RH of 44–66%. Separate experiments were

conducted at higher RH 70–85% for 30, 32, 35 and 40 °C (±0.1 °C); because no egg hatch was initially observed for these temperatures at previous RH 44–66%.

Eggs deposited were carefully isolated by cutting the section of leaf containing the egg and placed it singly on a 4.7-cm diameter dry filter paper in the aforementioned Petri dishes. One individual per Petri dish was considered a replicate and each temperature treatment had 50 replicates, except 10 °C at which 200 eggs were exposed. After egg hatching, its survival and incubation period was recorded. Larval instars were supplied daily with excess prey of all stages of TSSM by brushing infested bean leaves with a mite brushing machine. During larval development, cast exuviae observed were removed to determine the number of moults and the duration of each stage. Pupal survival and duration were also noted and recorded, accordingly.

A similar experimental setup was followed at fluctuating (12.7–32.1 °C) temperature. Petri-dishes were maintained in the well ventilated laboratory room. A temperature and relative humidity data logger (Tinytag, Hastings Data Loggers, Kempsey, NSW, Australia) was placed among the Petri dishes to log data hourly. Data were recorded as for the constant temperatures.

Statistical analysis

Mean developmental time of eggs, larvae and pupae, and all immature stages combined of S. vagans were calculated. Development rate for each life stage and all stages combined were derived by taking the reciprocal of mean development time (1/d). The relationships between temperature and developmental time were estimated by least-squares linear regression analysis in SAS (PROC REG, SAS Institute 1989). The lower developmental threshold temperatures for each specific stage as well as for all stages combined were derived from the regression equation at $a = 0.05$.

$$y = a + bx$$

(1) where $y$ is the developmental rate (expressed as 1/days) at temperature $x$ and $a$ and $b$ are estimates of the $y$ intercept and slope respectively (Sokal & Rohlf 1995). The degree-days (DD) were computed for development of each life stage and total stages using the method outlined by Price (1997):

$$DD = D (T-t)$$

(2) where DD degree-days needed for development at a specific temperature, $D$ mean numbers of days required for development at a certain temperature, $T$ temperature at which the development was observed, $t$ minimum threshold temperature for development. The mean DD required for development of each life stage was obtained by averaging its DD associated with all temperature regimes separately for eggs, larval instars and pupae. The mean DD for for S. vagans was calculated from the data obtained from all stages combined.

RESULTS

Developmental time

Developmental time of each life stage and all stages combined (egg-adult emergence) of S. vagans decreased as temperature increased. Mean total development times from egg to adult emergence at constant and fluctuating
temperatures (12.7–32.1 °C) are presented in Table 1. The egg developmental period varied from 16.5±0.8, at 12 °C and 2.2±0.3 days at 30 °C, although in the latter case eggs only hatched at higher relative humidity (70–85%). The egg incubation period recorded at fluctuating temperatures was 4.1±0.3 days. At 10 °C, eggs survived for a longer period without any embryonic development. Of the initial 200 eggs exposed to 10 °C for 60 days, none showed sign of development. However, more than 120 of these eggs hatched within the normal time period when they were subsequently exposed to ≥ 15 °C. At 35 °C eggs appeared to develop normally, but larvae died before or just after hatching. There were four larval instars, which were differentiated from each other by the presence of shed exoskeleton and differences in head capsule size (viz., larvae moulted three times before going to pupation). Mean duration of egg, all four larval instars, pupa and all stages combined at both constant and fluct-

**Table 1.** Development time (days, mean±SE) of immature stages of *S. vagans* at constant and fluctuating temperatures.

<table>
<thead>
<tr>
<th>Stage</th>
<th>n</th>
<th>12 °C</th>
<th>15 °C</th>
<th>20 °C</th>
<th>25 °C</th>
<th>30 °C</th>
<th>21.4 °C (12.7–32.1 °C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>96</td>
<td>16.5±0.8</td>
<td>9.9±0.7</td>
<td>5.2±0.5</td>
<td>3.8±0.4</td>
<td>2.2±0.3</td>
<td>4.1±0.3</td>
</tr>
<tr>
<td>1st instar larva</td>
<td>96</td>
<td>7.8±0.6</td>
<td>3.4±0.7</td>
<td>2.2±0.6</td>
<td>1.3±0.4</td>
<td>1.0±0.3</td>
<td>1.6±0.3</td>
</tr>
<tr>
<td>2nd instar larva</td>
<td>96</td>
<td>7.6±0.7</td>
<td>3.3±0.5</td>
<td>2.2±0.6</td>
<td>1.4±0.4</td>
<td>1.0±0.3</td>
<td>1.7±0.4</td>
</tr>
<tr>
<td>3rd instar larva</td>
<td>96</td>
<td>8.0±0.9</td>
<td>3.5±0.6</td>
<td>2.2±0.6</td>
<td>1.4±0.4</td>
<td>1.0±0.3</td>
<td>1.6±0.3</td>
</tr>
<tr>
<td>4th instar larva</td>
<td>96</td>
<td>9.1±0.6</td>
<td>3.6±0.5</td>
<td>2.2±0.7</td>
<td>1.6±0.4</td>
<td>1.2±0.3</td>
<td>1.7±0.3</td>
</tr>
<tr>
<td>Pupa</td>
<td>96</td>
<td>16.3±0.5</td>
<td>9.5±0.5</td>
<td>4.4±0.5</td>
<td>3.1±0.4</td>
<td>2.8±0.3</td>
<td>4.7±0.4</td>
</tr>
<tr>
<td>All stages combined</td>
<td>65.2±2.3</td>
<td>33.2±0.6</td>
<td>18.2±0.5</td>
<td>13.1±0.4</td>
<td>9.2±0.3</td>
<td>15.4±0.3</td>
<td></td>
</tr>
</tbody>
</table>

**Table 2.** Rate of development of immature stages of *S. vagans* at constant and fluctuating temperatures (proportion/day).

<table>
<thead>
<tr>
<th>Stages</th>
<th>12 °C</th>
<th>15 °C</th>
<th>20 °C</th>
<th>25 °C</th>
<th>30 °C</th>
<th>21.4 °C (12.7–32.1 °C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>0.061</td>
<td>0.100</td>
<td>0.193</td>
<td>0.260</td>
<td>0.459</td>
<td>0.246</td>
</tr>
<tr>
<td>1st instar</td>
<td>0.129</td>
<td>0.298</td>
<td>0.463</td>
<td>0.752</td>
<td>1.031</td>
<td>0.600</td>
</tr>
<tr>
<td>2nd instar</td>
<td>0.132</td>
<td>0.303</td>
<td>0.474</td>
<td>0.709</td>
<td>1.041</td>
<td>0.559</td>
</tr>
<tr>
<td>3rd instar</td>
<td>0.125</td>
<td>0.286</td>
<td>0.463</td>
<td>0.694</td>
<td>0.962</td>
<td>0.617</td>
</tr>
<tr>
<td>4th instar</td>
<td>0.110</td>
<td>0.277</td>
<td>0.459</td>
<td>0.610</td>
<td>0.806</td>
<td>0.578</td>
</tr>
<tr>
<td>Pupa</td>
<td>0.062</td>
<td>0.105</td>
<td>0.226</td>
<td>0.293</td>
<td>0.360</td>
<td>0.215</td>
</tr>
<tr>
<td>All stages</td>
<td>0.015</td>
<td>0.030</td>
<td>0.055</td>
<td>0.077</td>
<td>0.109</td>
<td>0.065</td>
</tr>
</tbody>
</table>

**Table 3.** Regression of rate of development (1/y) with calculated values of correlation coefficient (r), probability (P), and minimum threshold temperature of development (t) at constant temperatures. ***: P < 0.001.

<table>
<thead>
<tr>
<th>Stages</th>
<th>Regression equations</th>
<th>r</th>
<th>t (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>$Y = -0.21223 + 0.02092x$</td>
<td>0.98***</td>
<td>10.14</td>
</tr>
<tr>
<td>1st instar</td>
<td>$Y = -0.46514 + 0.04898x$</td>
<td>0.99***</td>
<td>9.50</td>
</tr>
<tr>
<td>2nd instar</td>
<td>$Y = -0.46034 + 0.04855x$</td>
<td>0.98***</td>
<td>9.48</td>
</tr>
<tr>
<td>3rd instar</td>
<td>$Y = -0.4076 + 0.04478x$</td>
<td>0.99***</td>
<td>9.10</td>
</tr>
<tr>
<td>4th instar</td>
<td>$Y = -0.30784 + 0.03735x$</td>
<td>0.99***</td>
<td>8.24</td>
</tr>
<tr>
<td>Pupa</td>
<td>$Y = -0.13447 + 0.01689x$</td>
<td>0.98***</td>
<td>7.96</td>
</tr>
<tr>
<td>All stages</td>
<td>$Y = -0.04655 + 0.00509x$</td>
<td>0.99***</td>
<td>9.07</td>
</tr>
</tbody>
</table>

Fluctuating temperatures are shown in Table 1. There were significant differences in all immature stages combined and for stage specific development times at different temperatures (p < 0.05) (Table 3).

**Developmental rate**

The reciprocals of mean development time in days at both constant and fluctuating temperatures were calculated as a percentage of developmental rates per day (Table 2). The development rate for each stage and for all stages combined increased as the temperature increased. The development rate of the egg stage increased from 6.1% per day at 12 °C to 46% per day at 30 °C. The daily rate recorded for all four larval instars combined was 18% per day at 12 °C and 96% per day at 30 °C, and was 6.2% and 36% per day for the pupal stage at the same temperatures, respectively. The daily rate of development for eggs, larval and pupal stages was 24.6, 60.1, and 21.5%, respectively, at fluctuating temperatures. The mean daily development was 0.06 and 0.36%, at 12 and 30 °C constant, and 0.21% at fluctuating temperatures (12.7–32.1 °C).

The relations between mean developmental rate and temperature were determined for each stage and for all immature stages combined (Table 3). Based on the linear regression equations the lower developmental threshold temperatures were estimated to be 10.1, 9.5, 9.5, 9.1, 8.2, and 8.0 °C for egg, 1st, 2nd, 3rd, 4th instars, and pupal stages, respectively. The mean lower developmental threshold temperatures for all stages combined was 9.1 °C.

The parameters of the linear regression (intercept and slope) described the relationship between the developmental rate (y) and temperature (x) for each stage and for all stages combined in *S. vagans*. The correlation coefficient (r) for each stage and all stages combined was very high (from 0.98 to 0.99) indicating a good fit of data to the linear degree-days model within the tem-
Development of Stethorus Vagans (Coleoptera: Coccinellidae)

Table 4. Degree-days (DD) needed for development of immature stages of S. vagans at constant and fluctuating temperatures.

<table>
<thead>
<tr>
<th>Stages</th>
<th>Constant temperature</th>
<th>Fluctuating temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>12 °C</td>
<td>15 °C</td>
</tr>
<tr>
<td>Egg</td>
<td>47.91</td>
<td>58.47</td>
</tr>
<tr>
<td>1st instar larva</td>
<td>22.53</td>
<td>19.82</td>
</tr>
<tr>
<td>2nd instar larva</td>
<td>21.92</td>
<td>19.47</td>
</tr>
<tr>
<td>3rd instar larva</td>
<td>23.20</td>
<td>20.65</td>
</tr>
<tr>
<td>4th instar larva</td>
<td>26.48</td>
<td>21.30</td>
</tr>
<tr>
<td>Pupa</td>
<td>47.15</td>
<td>56.05</td>
</tr>
<tr>
<td>All stage</td>
<td>189.94</td>
<td>195.76</td>
</tr>
</tbody>
</table>

Temperature range of 12 to 30 °C (Table 3). There were no significant differences among immature stages at lower development temperature threshold as their 95% confidence intervals overlapped broadly. Therefore, the lower threshold temperature for all stages combined was used to determine the number of degree-days required to complete development for each stage and for all immature stages combined.

Degree Day (DD)

Degree-days (DD) requirements of S. vagans were calculated for each stage and for all immature stages combined from the developmental data and mean threshold developmental temperature 9.1 °C. Total mean DD estimated for development from egg to adult emergence and individual DD computed for egg, larval instars and pupal stages for constant and fluctuating temperature are presented in Table 4. DD calculated for the four larval instars ranged from 19.5 to 26.5 per instar over the range of constant and fluctuating temperatures, while for the pupal stage it varied from 47.2 to 58.1 DD at the same temperatures.

Discussion

This study is the first to investigate the effect of constant and fluctuating temperatures on the development of S. vagans. Information on developmental time, rate and thermal characteristics of this potential predator was gathered during this research. These data on S. vagans will be important for the development of forecast models to understand temperature ranges which affect
development and survival of this potential predator and its synchronization with its host.

Effect of temperature on the development of S. vagans

In this study, development occurred at all temperatures except at very low (10 °C) or high temperatures (35 and 40 °C). Therefore these extreme temperatures were outside the temperature range (12–32 °C) required for the development of S. vagans. Development did not appear at the aforementioned low temperature, but the eggs remained viable and hatched within a normal timeframe when exposed to ≥15 °C. Similarly, at higher temperature (35 °C) embryos developed within the egg, but died before or just after hatching. Our laboratory finding is supported by the results recorded for ambient temperatures for presence of this predator in the field. Our results are also partially in conformity with Putman (1955) and Roy et al. (2002), who reported that S. punctillum eggs did not hatch at 12 and 36 °C.

Developmental time decreased linearly with increased temperatures within the range 12–32 °C for all immature stages (including eggs) of S. vagans. For instance, it took 65.2 days at 12 °C and 9.2 days at 30 °C constant, which was a little more than those reported by Richardson (1977) for S. loxtoni (52.3 and 8.3 days) at constant temperatures of 15 and 30 °C, respectively. This slight difference in development rates between these two Australian species may be due to the fact that S. vagans commonly occurs in coastal and sub-coastal climates, while S. loxtoni is more common in the inland and Mediterranean climate areas (Britton & Lee 1972, Readshaw 1975). On the other hand the total developmental time for S. vagans is shorter than for S. punctillum (68.5 and 12 days at 14 and 34 °C, respectively) as indicated by Roy et al. (2005) and S. gilvifrons (56.47 and 9.27 at 15 and 35 °C, respectively) (Taghzadeh et al. 2008). In our study the total development time of S. vagans fed on T. urticae at 25°C was 13.1 days, compared with 15.3 days for S. loi at 23.8 °C when fed on T. knizavai (Shin et al. 1991), 17 days for S. punctillum at 24 °C fed on T. mcdanieli, and 18.5 days for S. gilvifrons at 25 °C on T. urticae. The reason may be that S. vagans is smaller and adapted to different climatic zones than the above species; the other possible reason is that majority of them have different primary hosts.

Developmental time for individual immature stages of our study insect was also generally shorter than other species of the same genus. Mean development time for S. vagans eggs (9.9 days at 15 °C and 2.2 days at 30 °C) was different than that reported by Richardson (1977) for S. loxtoni (14.3 days at 15 °C and 1.9 days at 30 °C), and for S. gilvifrons (13.0 days at 30 °C) (Taghzadeh et al. 2008). Larval stages of the most of the aforementioned Stethorus

species also took longer to complete. While these differences might reflect different species characteristics, one of the other possible reasons that we studied the development of *S. vagans* in small Petri dishes, which has a larger area than Munger cells in which the other species that were studied. Another possible reason is that some of the other species of *Stethorus* were fed on a different species of prey mites.

The overall lower developmental threshold for all immature stages combined was estimated to be 9.07 °C for *S. vagans*. Peterson et al. (1994) reported a threshold temperature of 10.5 °C for *S. bifidus*, and Roy et al. (2005) for *S. punctillum* and Taghizadeh et al. (2008) for *S. gilvifrons* demonstrated similar lower threshold temperatures. The differences among these results may be due to different species studied from different parts of the world and their different hosts. However, the overall consistency of the data confirms that temperature has significant effects on the development of *Stethorus* species.

The lower developmental threshold temperature for individual immature stages of *S. vagans* was 10.1, 9.5, 9.1, 8.2, 8.0, and 9.1 °C for egg, 1st, 2nd, 3rd, 4th larval instars, pupa and all stages combined, respectively. The threshold temperature for the egg stage was higher than the rest of immature stages of *S. vagans*. This may have been possibly due to leaf structure and humidity in the cell, because the eggs were kept with the portion of leaf on which they were laid, while other immature stages were reared directly on dry filter paper. However, differences in threshold temperatures for different immature stages are not uncommon in insect species. For example, Richardson (1977) recorded different lower threshold temperatures for different immature stages of *S. loxoni*, with the highest (11.5 °C) being for the egg stage and lowest (6.5 and 6.0 °C, respectively) for 2nd and 3rd instars. Our results also agreed with the observations recorded for *S. bifidus*, which has lower threshold temperatures of 11.9 °C for the egg stage and 9.4 °C for 3rd instar larvae (Peterson et al. 1994). A similar difference in lower threshold temperatures within various stages was reported for *S. gilvifrons* with 14.11 °C for egg stage, while the lowest was 5.20 °C for 1st instar larvae (Taghizadeh et al. 2008). Savopoulos-Sultani (1997) also reported different threshold temperatures from 8.2 to 15.4 °C for different immature stages of euonymus scale, *Euonymus japonica* and Nordin and O’Canna (1985) recorded different lower thresholds for stages of the fall webworm, *Hyphantria cunea* at 14, 11, and 12 °C for egg, larva, and pupal stages, respectively.

The lower developmental threshold temperature we recorded for the egg stage appears to be valid, based on the data showing that eggs did not develop at 10 °C, although they remained viable for a long time (60 days), and subsequently hatched in the normal time period when exposed to temperatures of ≥15 °C. This characteristic may enable this species to survive winter.
in the egg stage and hatch when temperature becomes favorable. However, in the field very few eggs appear to hatch in winter even when the temperature rises above from 10 °C, because field counts during a two year period indicated that the number of motile *S. vagans* declined under these conditions (Khan 2001).

Van de Vrie et al. (1972) calculated a lower threshold temperature of 10 °C for *T. urticae*, while Readshaw (1975) reported a lower threshold of around 9 to 10 °C for eggs and immature stages of this mite species. Therefore the lower threshold temperatures of prey and predator are in harmony. The developmental period we recorded for *S. vagans* from egg to egg was 43.8, 23.6 and 10.3 days at 15, 20 and 30 °C, respectively, and was longer than *T. urticae* developmental period, which was 36.4, 16.6 and 7.3 days at the aforementioned temperatures (Khan 2001, Bower & Thwaite 1995). The oviposition rate recorded for *T. urticae* was also higher i.e. 200 eggs at a rate of 3–14 eggs /female /day in their life span of 3–4 weeks (Bower & Thwaite 1995). However the rate of predation of by *S. vagans* larvae and adults was much higher than the rate of *T. urticae* oviposition and development (i.e. larval instars 27.9–152 eggs /day, adult males and ovipositing females 63.5–142.7 eggs/day) (Bower & Thwaite 1995, Khan 2001).

Eggs of *S. vagans* developed into larvae at a constant temperature of 35 °C, but they could not survive for a long time. The temperature during summers in the Hawkesbury valley, New South Wales, Australia does not rise often above 35 °C. On the other hand, temperatures in the microclimate within trees, plants and shrubs are lower than the normal ambient temperature, which is likely to provide a suitable environment for *S. vagans* stages to survive and reproduce.

**Degree Days (DD)**

The degree-days (DD) model is the most widely used approach for describing insect development rate and in predicting insect developmental times as a function of temperature. There were slight differences between the DD calculations for immature stages and all stages combined resulted from data generated at different constant and fluctuating temperatures. These slight differences may be due to temperature fluctuations occurring when they were removed from the designated temperature for observation, although this time was tried to be minimized. However, differences in DD within the life stages of insect species at constant and fluctuating temperatures have been reported by a number of authors. For example, Hanula et al. (1987) observed different DD for immature stages of pine cone worm, *Diorystria amatella*, at different constant and fluctuating temperatures. Tolley and Neimczyk (1988) also re-
ported a deal of variation in DD for the fruit fly, *Oscinella frit*, calculated from eight constant temperatures. Our results (207.8 DD) observed at a constant 25 °C for all stages combined of *S. vagans* are quite close to that recorded for all stages combined of *S. bifidus* (217 DD) and *S. glisifrons* (222.72 DD) estimated at a constant 27.5 °C and 28 °C, respectively (Peterson et al. 1994, Taghzadeh et al. 2008).

Threshold temperature and DD for the development of the predators can play a significant role in the selection of potential predators, which can be used in various ecological zones (Perdikis & Lykouressis 2002). The lower threshold temperature and thermal constant have been estimated from simple linear models for a number of insect pests and their natural enemies (Roy et al. 2005).

In conclusion, this study describes the temperature-dependent development relationship of an Australian population of *S. vagans* at a range of constant and fluctuating temperature commonly occurs in coastal and sub-coastal climates. This study can be helpful in predicting *S. vagans* population development in the field. Information from this study can be used for its mass rearing, predation studies, thermal adaptation, and optimizing synchronization of the predator and its host. Furthermore, this information can be incorporated in IPM programs for the management of *T. urticae* in field and green house crops.

REFERENCES


Fan, F., Groden, E. & Drummond, F. A. (1992): Temperature dependent development of Mexican bean beetle (Coleoptera: Coccinellidae) under constant and variable tem-


Michels-Jr, G. J. & Behle, R. W. (1991): Effect of two prey species on the development of Hippodamia sinuata (Coleoptera: Coccinellidae) larvae at two constant temper-


Received May 20, 2015, accepted October 24, 2015, published March 3, 2017