

Influence of prey species on immature survival, development, predation and reproduction of *Coccinella transversalis* Fabricius (Col., Coccinellidae)

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Abstract: Six aphid species, viz. *Aphis craccivora*, *Aphis gossypii*, *Aphis nerii*, *Myzus persicae*, *Lipaphis erysimi* and *Uroleucon compositae* were provided as prey to the feeding stages of *Coccinella transversalis* (Fabricius). All of them were found to be essential prey, however the relative prey suitability varied. All the predatory stages of *C. transversalis* consumed and preferred *A. gossypii*, the most and *A. nerii*, the least. Significant effect of prey quality was observed on pre-imaginal developmental periods, wet weights and adult longevity. The complete development was shortest on *A. gossypii* (13.01 ± 0.18 days) and longest on *A. nerii* (20.51 ± 0.25 days). The total prey consumption by larva, adult male and female in their lifetime was maximum (665.30 ± 5.75 , 4831.10 ± 123.54 and 5412.30 ± 94.51 , respectively) on *A. gossypii* and minimum (434.80 ± 4.03 , 802.80 ± 34.37 and 905.20 ± 52.48 , respectively) on *A. nerii*. Immature survival, growth index and adult emergence of *C. transversalis* was maximum (68.33, 7.82 and 88.21%, respectively) when larval instars consumed *A. gossypii* and minimum (37.75, 2.18 and 60.69%, respectively) after feeding on *A. nerii*. Female reproduction was also prey quality dependent showing maximum reproductive performance in terms of fecundity and percentage viability, with a highest reproductive period and lowest non-reproductive period on *A. gossypii*, followed by *A. craccivora*, *L. erysimi*, *M. persicae*, *U. compositae* and *A. nerii*. Regression analysis revealed a positive correlation between: (1) daily prey consumption and relative growth rate, (2) adult weight and developmental rate, (3) weights of adult male and female, and (4) female longevity and fecundity.

Key words: *Coccinella transversalis*, prey, aphid, immature, survival, predation, reproduction

1 Introduction

Coccinella transversalis Fabricius is a predaceous ladybeetle native to India and abundant in South Asia (OMKAR and PERVEZ, 2000). It is commonly found preying on aphids, *Aphis craccivora* Koch, *Aphis gossypii* Glover and *Lipaphis erysimi* (Kaltenbach) in agricultural and horticultural fields (OMKAR and BIND, 1993), and is one of the important members of the local predator complex. Its wide prey range and acceptance of a variety of aphid species, suggests its potential as a biocontrol agent in aphid management programmes (OMKAR et al., 1999). The predatory potential of *C. transversalis* has been well documented in some recent publications (BABU, 1999; OMKAR et al., 1999; DEBRAJ and SINGH, 2000; EVANS, 2000; GEORGE, 2000; OMKAR and JAMES, 2001). However its growth, development and reproduction remain relatively unassessed.

The potential of a biocontrol agent is assessed not only in terms of its predatory potential but also in its adaptability to new surroundings deciphered through its ability to propagate itself under a given condition including the prey. For this purpose the growth,

development, survival and reproduction of the ladybirds on potential prey needs to be assessed in the laboratory. Prey have been categorized into accepted, essential and rejected on the basis of their suitability to the ladybirds, assessed on the basis of their principal developmental and reproductive attributes (HODEK and HONEK, 1996). The present investigations have been, thus, designed to identify the prey species most suitable for the growth, development and reproduction of *C. transversalis*. The information so obtained can be further exploited for the mass multiplication of *C. transversalis* as also the identification of appropriate species from six locally abundant aphid species.

2 Materials and Methods

2.1 Stock culture

Adults of *C. transversalis* were collected from the agricultural fields adjoining the city of Lucknow, India, and brought to the laboratory. Mating pairs were selected and kept together

in separate glass jars (diameter 11.0 cm and 8.5 cm), and provided six different aphid species, viz. *A. craccivora*, *A. gossypii*, *Aphis nerii* Boyer de Fonsclombe, *Myzus persicae* (Sulzer), *L. erysimi* and *Uroleucon compositae* (Theobald) infested on host plant twigs, viz. *Dolichos lablab* Linnaeus, *Lagenaria vulgaris* Seringe, *Calotropis procera* (Aiton), *Solanum tuberosum* Linnaeus, *Brassica campestris* Linnaeus and *Carthamus tinctorius* Linnaeus, respectively as prey at $25 \pm 2^\circ\text{C}$ and $65 \pm 5\%$ RH. After mating, the females laid large batches of eggs, which were removed from the culture and kept separately. The eggs were removed after every 24 h. The dried twigs and leftover aphids were replenished after every 24 h to avoid any microbial contamination.

2.2 Experiment design

2.2.1 Pre-imaginal development and immature survival

The prey species-dependent pre-imaginal development and immature survival of *C. transversalis* were investigated and for this, 100 eggs each were selected from the stock maintained at different prey species level and kept in the Petri dishes (diameter 16.0 cm and height 2.6 cm), which were then kept in an environmental test chamber maintained at 27°C and $65 \pm 5\%$ RH. After the hatching of first instars from the eggs, the incubation period and number of first instars hatched were recorded. The tiny first instars were taken out from the Petri dishes and transferred into glass beakers (height 11.0 cm and diameter 9.0 cm) (10 instars per beaker) with the help of a soft camel hairbrush (no. zero). The open ends of tubes were covered with fine muslin cloths fastened with rubber bands. First instars from egg batches on different aphid species were supplied with the same aphid species (70 mg wet weight) as provided to their parental generation. The leftover aphids and host plant twigs were replenished daily to avoid contamination and microbial infection. When ecdyses occurred, the first instar duration and survival were recorded. Similarly, the duration and survival of later instars were recorded. Thereafter, pre-pupal and pupal periods along with their survival were also recorded. The experiment was performed in 10 replicates ($n = 10$).

Percentage immature survival (number of pupae \times 100/number of first instars hatched), adult emergence (number of adults emerged \times 100/number of pupae) and development rate (1/developmental period, i.e. the period from the day of oviposition to adult emergence) were recorded. Growth index (i.e. ratio of percentage pupation and mean larval duration) was calculated following DUBEY et al. (1981).

Different life stages such as four different instars, pupal stages (pre-pupa and pupa) and adults (male and female) were weighed separately in 10 replicates ($n = 10$) using electronic balance. The relative growth rate was calculated using the formula:

Relative growth rate =

$$\frac{\text{Initial adult weight (mg)} - \text{Initial weight of fourth instar (mg)}}{\text{Developmental period (in days)}}$$

2.3 Larval and adult consumption on different aphid species

The newly hatched first instars were daily supplied with 100 aphid individuals of each species until they moulted. Similarly, newly moulted second, third and fourth instars were daily provided with 100, 400 and 400 individuals of different aphids, respectively, until the next moulting (or pupal phase). Data on the prey consumption were recorded. The newly

eclosed adults were provided with 200 aphids daily for their lifetime and their total and mean aphid consumption were calculated. The data were recorded in 10 replicates ($n = 10$). Early instars of larger aphids, viz. *A. craccivora* and *U. compositae* and later instars of smaller aphids, viz. *A. gossypii*, *A. nerii*, *L. erysimi* and *M. persicae*, were selected to standardize the prey size. Gravid females of aphids were discarded.

2.4 Reproductive attributes of *C. transversalis* on different aphid species

Six sets of newly eclosed adults were paired and provided with the above-mentioned six aphid species for their lifetime with daily replenishment of fresh aphids (70 mg wet weight) infested on host plant twigs. After the pre-oviposition period, the female laid eggs continuously during the course of oviposition period. The eggs were counted and separated from the adults. The data on the pre-oviposition, oviposition and post-oviposition periods, fecundity, percentage egg viability and adult (male and female) longevity were recorded. The mean reproductive rate was calculated by taking into account the ratio of fecundity and ovipositional period. The experiment was performed in 10 replicates ($n = 10$).

2.5 Data analysis

The data obtained from the above experiments were statistically analysed using one way ANOVA and comparison of means was made using Bonferroni's method following the statistical package Statistix 4.1 (1994) on PC. Regression analysis was applied to determine the relationships between: (1) daily prey consumption and relative growth rate, (2) development rate and weight of adults, (3) the log weight of male and female, and (4) longevity and fecundity.

3 Results

3.1 Pre-imaginal development and immature survival

The duration and weight of different life stages of *C. transversalis* when provided with six aphid species are listed in table 1. The significant effect of the various aphid foods were observed on all the life stages. This include incubation period ($F = 36.35$; $P < 0.001$), first ($F = 18.37$; $P < 0.001$), second ($F = 35.85$; $P < 0.001$), third ($F = 25.85$; $P < 0.001$) and fourth instars ($F = 15.68$; $P < 0.001$), pre-pupal ($F = 6.99$; $P < 0.001$) and pupal periods ($F = 40.06$; $P < 0.001$). Total development period was thus cumulatively affected by the significant integral components, and was highly significant ($F = 228.03$; $P < 0.001$). The complete development was shortest on *A. gossypii* (13.01 ± 0.18) and longest on *A. nerii* (20.51 ± 0.25).

Significant variation was observed in the weight of different predatory stages, after feeding on six aphid species (table 1). The overall wet weights of first ($F = 68.98$; $P < 0.001$), second ($F = 44.87$; $P < 0.001$) and third ($F = 178.36$; $P < 0.001$) instars were significant. However, when the mean values of the weights at different prey levels were compared, some of them did not vary significantly. The weight of fourth instars ($F = 141.74$; $P < 0.001$), pre-pupae ($F = 581.38$; $P < 0.001$) and pupae ($F = 206.35$;

Table 1. Duration (in days) and weight (in mg) of different life stages of *Coccinella transversalis* on six aphid species ($n = 10$)

| Aphid species | <i>A. gossypii</i> | <i>A. craccivora</i> | <i>L. erysimi</i> | <i>M. persicae</i> | <i>U. compositae</i> | <i>A. nerii</i> | F-value* |
|-------------------|--------------------|----------------------|-------------------|--------------------|----------------------|-----------------|----------|
| Incubation period | | | | | | | |
| Duration | 2.01 ± 0.03 | 2.37 ± 0.06 | 2.66 ± 0.06 | 2.91 ± 0.10 | 3.11 ± 0.11 | 3.33 ± 0.10 | 36.35 |
| First instar | | | | | | | |
| Duration | 1.74 ± 0.09 | 1.99 ± 0.11 | 2.19 ± 0.09 | 2.35 ± 0.08 | 2.53 ± 0.08 | 2.71 ± 0.05 | 18.37 |
| Weight | 2.77 ± 0.09 | 2.19 ± 0.04 | 1.96 ± 0.04 | 1.65 ± 0.09 | 1.40 ± 0.08 | 1.21 ± 0.04 | 68.98 |
| Second instar | | | | | | | |
| Duration | 1.51 ± 0.07 | 1.74 ± 0.04 | 1.99 ± 0.11 | 2.19 ± 0.05 | 2.37 ± 0.05 | 2.56 ± 0.05 | 35.85 |
| Weight | 5.78 ± 0.12 | 5.17 ± 0.03 | 5.10 ± 0.06 | 4.94 ± 0.04 | 4.65 ± 0.12 | 4.25 ± 0.04 | 44.87 |
| Third instar | | | | | | | |
| Duration | 1.79 ± 0.05 | 1.94 ± 0.09 | 2.17 ± 0.09 | 2.43 ± 0.12 | 2.68 ± 0.09 | 2.98 ± 0.08 | 25.85 |
| Weight | 9.33 ± 0.30 | 9.03 ± 0.06 | 8.48 ± 0.12 | 8.10 ± 0.06 | 7.15 ± 0.05 | 6.08 ± 0.16 | 178.36 |
| Fourth instar | | | | | | | |
| Duration | 2.67 ± 0.06 | 2.91 ± 0.02 | 3.09 ± 0.10 | 3.26 ± 0.09 | 3.55 ± 0.12 | 3.77 ± 0.16 | 15.68 |
| Weight | 16.82 ± 0.04 | 16.09 ± 0.06 | 14.94 ± 0.13 | 14.33 ± 0.15 | 13.99 ± 0.05 | 12.59 ± 0.22 | 141.74 |
| Pre-pupa | | | | | | | |
| Duration | 0.80 ± 0.03 | 0.93 ± 0.01 | 1.06 ± 0.05 | 1.17 ± 0.12 | 1.23 ± 0.07 | 1.36 ± 0.12 | 6.99 |
| Weight | 14.57 ± 0.11 | 13.64 ± 0.18 | 12.84 ± 0.09 | 12.01 ± 0.04 | 10.76 ± 0.16 | 10.00 ± 0.07 | 581.38 |
| Pupa | | | | | | | |
| Duration | 2.49 ± 0.09 | 2.68 ± 0.04 | 2.99 ± 0.10 | 3.31 ± 0.06 | 3.56 ± 0.08 | 3.80 ± 0.09 | 40.06 |
| Weight | 13.08 ± 0.07 | 12.36 ± 0.15 | 11.87 ± 0.13 | 10.94 ± 0.11 | 9.60 ± 0.06 | 9.08 ± 0.12 | 206.35 |
| Development | | | | | | | |
| Duration | 13.01 ± 0.18 | 14.55 ± 0.19 | 16.28 ± 0.13 | 17.40 ± 0.19 | 19.01 ± 0.16 | 20.51 ± 0.25 | 228.03 |
| Weight | 22.67 ± 0.23 | 20.33 ± 0.11 | 17.29 ± 0.12 | 16.02 ± 0.08 | 14.66 ± 0.09 | 13.93 ± 0.12 | 622.05 |
| Male | | | | | | | |
| Female | 29.28 ± 0.14 | 27.73 ± 0.17 | 25.38 ± 0.16 | 22.99 ± 0.07 | 21.13 ± 0.16 | 18.92 ± 0.11 | 806.89 |

Values are mean ± SE.
* Significant at $P < 0.001$.

$P < 0.001$) varied significantly when the fourth instars were fed on six aphid prey. Adult males ($F = 622.05$; $P < 0.001$) and females ($F = 806.89$; $P < 0.001$) showed significant variation in weights when fed on different aphid species.

The relative growth rate and the developmental rate of the ladybeetle was maximum on *A. gossypii* and minimum on *A. nerii* (table 3). Percentage immature survival, growth index and percentage adult emergence of *C. transversalis* was maximum (68.33, 7.82 and 88.21, respectively) when the larval instars were fed on *A. gossypii* and minimum (37.75, 2.18 and 60.69, respectively) after feeding on *A. nerii*. The regression analysis revealed a positive correlation between female weight and the developmental rate on six aphid species. The regression equation was $Y = 1.56 + 372X$; $r = 0.98$; $P < 0.001$ (fig. 1b). Similarly, the female weight was also positively correlated with the weight of male ladybeetle giving the regression equation $Y = 4.46 + 1.13X$; $r = 0.97$; $P < 0.001$ (fig. 1c).

3.2 Larval and adult consumption on different aphid species

Lifetime prey consumption by the predatory stages and the mean daily prey consumption by the adult male and female ladybeetles on the six aphid species are presented in table 2. Significant aphid consumption by each predatory stage was observed with a maximum consumption of *A. gossypii* followed by *A. craccivora*, *L. erysimi*, *M. persicae*, *U. compositae* and a minimum of *A. nerii*. Prey consumption by first ($F = 79.52$; $P < 0.001$), second ($F = 112.11$; $P < 0.001$), third ($F = 108.05$; $P < 0.001$) and fourth

($F = 205.47$; $P < 0.001$) instars differed significantly, also resulting in significant total larval consumption ($F = 375.37$; $P < 0.001$). Amongst adults significant difference in lifetime prey consumption was observed by adult male ($F = 285.04$; $P < 0.001$) and female ladybeetles ($F = 368.30$; $P < 0.001$). The mean aphid consumption by adult male ($F = 184.91$; $P < 0.001$) and female ($F = 195.13$; $P < 0.001$) ladybeetles on six aphid species was also significant. Regression analysis revealed a positive correlation between daily prey consumption and relative growth rate. The regression equation for daily prey consumption and relative growth rate was $Y = 8.50 + 60.1X$; $r = 0.97$; $P < 0.001$ (fig. 1a).

3.3 Reproduction on different aphid species

Data on the reproductive attributes of *C. transversalis*, expressed in pre-oviposition, oviposition and post-oviposition periods, fecundity, percentage viability of eggs, mean reproductive rate and adult longevities when fed on six aphid species are presented in table 3. Significant variations in pre-oviposition period ($F = 33.41$, $P < 0.001$), oviposition period ($F = 225.10$, $P < 0.001$), ($F = 27.87$; $P < 0.001$), fecundity ($F = 291.90$, $P < 0.001$) and percentage viability of eggs ($F = 38.22$, $P < 0.001$) were recorded. The mean reproductive rate of the female ladybeetle was maximum on *A. gossypii* and minimum on *A. nerii*. The longevity of male ($F = 154.04$, $P < 0.001$) and female ($F = 160.50$, $P < 0.001$) ladybeetles varied significantly with maximum (81.60 ± 1.54 and 86.10 ± 0.19 , respectively) on *A. gossypii* and minimum (39.70 ± 0.75 and 41.90 ± 0.75 , respectively)

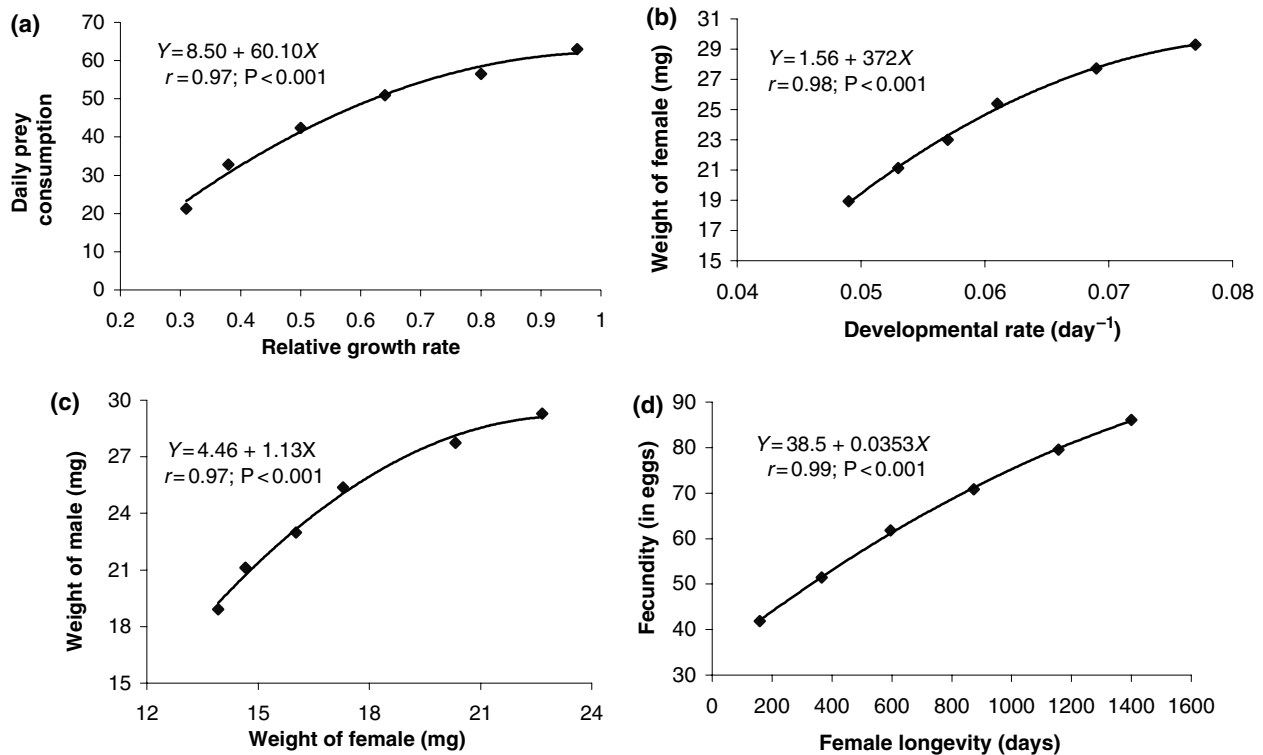


Fig. 1. Best fit lines showing relationships between (a) daily prey consumption and relative growth rate, (b) weight of female and developmental rate, (c) weights of male and female, and (d) fecundity and female longevity of *Coccinella transversalis* on different aphid species ($n = 10$)

on *A. nerii*. Regression analysis revealed a positive correlation between female longevity and fecundity. The regression equation was $Y = 38.5 + 0.0353X$; $r = 0.99$; $P < 0.001$ (fig. 1d).

4 Discussion

4.1 Pre-imaginal development and immature survival

The results reveal that all the six aphid species are the essential foods for the immature survival and development of *C. transversalis*. Of these, *A. gossypii* is the most suitable aphid species followed by *A. craccivora*, *L. erysimi*, *M. persicae*, *U. compositae* and *A. nerii*. Although aphids of equal wet weights were provided to predatory stages yet differential development and survival was observed. This may be attributed to the difference in the consumption, utilization as well as assimilation. The increased developmental rate of neonate instars on *A. gossypii* may be due to its increased preference and consumption. The decreased consumption of lesser preferred prey species may lead to a state of semi-starvation and this may also be a cause of the slower pre-imaginal development and decreased immature survival (KAWAUCHI, 1979). Other than this, the probable high and suitable nutrient contents of *A. gossypii* over other aphid species for *C. transversalis* may be a reason for the significant preference.

Significant effect of parental diet (quantity and quality) has been observed on embryogenesis, resulting in an expedited hatching to those eggs whose parents

were fed on *A. gossypii*. Thus, it can be inferred that the quality and quantity of aphid consumed have substantial effect on larval development.

The rapid development rate on *A. gossypii* is probably a result of the increased consumption and better nutritive quality. Relative growth rate of the ladybeetle, referring to aphid biomass conversion of predator, was found to be directly proportional to the amount of food eaten.

The preference of the prey is also dependent on its host plant (AZAM and ALI, 1970; OBATAKE and SUZUKI, 1985). The suitability of *A. gossypii* indicates that the host plant used in this experiment, viz. *L. vulgaris* is also suitable and does not cause any detrimental effects.

Weights of later instars, pupae and adults varied more significantly than the weights of neonates and early instars, when active stages fed on different aphid species. This might be ascribed to the fact that neonates and early instars consumed less prey, whereas later stages consumed more food owing to high energy requirement to attain a critical weight needed for ecdyses and pupation. The later instars were more specific towards the prey choice attaining more significant critical weights. The pre-pupae were heavier than pupae, owing to biochemical changes during the metamorphosis of pre-pupae into the pupae. The possible energy consumption and metabolic activities in the pupal stage at the cost of ladybeetle biomass may be a reason for this decrease in the weight of pupa. SIDHU and MUKESH (1979) observed the presence of more number of substances in the pre-pupae, which were responsible for the comparative heavier weight of pre-pupae than pupae.

Table 2. Prey consumption by predatory stages of *Coccinella transversalis* on six aphid species ($n = 10$)

| Aphid species | <i>A. gossypii</i> | <i>A. craccivora</i> | <i>L. erysimi</i> | <i>M. persicae</i> | <i>U. compositae</i> | <i>A. nerii</i> | F-value* |
|----------------------------|--------------------|----------------------|-------------------|--------------------|----------------------|-----------------|----------|
| First instar consumption | 31.80 ± 0.68 | 26.04 ± 0.78 | 22.10 ± 1.29 | 17.60 ± 0.67 | 15.40 ± 0.58 | 13.50 ± 0.45 | 79.52 |
| Second instar consumption | 63.60 ± 1.08 | 58.40 ± 0.93 | 52.60 ± 1.19 | 43.90 ± 1.22 | 39.30 ± 1.43 | 32.00 ± 0.90 | 112.11 |
| Third instar consumption | 166.50 ± 2.75 | 153.30 ± 1.76 | 137.40 ± 1.43 | 131.00 ± 1.50 | 125.80 ± 2.09 | 109.60 ± 1.92 | 108.05 |
| Fourth instar consumption | 403.40 ± 3.41 | 388.30 ± 2.54 | 360.60 ± 2.43 | 337.70 ± 2.69 | 315.20 ± 2.32 | 274.70 ± 3.30 | 205.47 |
| Total larval consumption | 665.30 ± 5.75 | 626.40 ± 3.53 | 572.70 ± 2.99 | 530.20 ± 3.05 | 495.70 ± 4.99 | 434.80 ± 4.03 | 375.37 |
| Daily consumption (male) | 59.20 ± 0.98 | 52.33 ± 1.08 | 46.80 ± 1.39 | 38.50 ± 0.96 | 30.90 ± 0.89 | 20.30 ± 0.98 | 184.91 |
| Daily consumption (female) | 62.98 ± 1.01 | 56.50 ± 1.40 | 50.90 ± 1.12 | 42.38 ± 1.03 | 32.80 ± 1.04 | 21.20 ± 1.11 | 195.13 |
| Total consumption (male) | 4831.10 ± 123.54 | 3883.70 ± 81.95 | 3068.70 ± 130.50 | 2161.40 ± 61.93 | 1435.70 ± 72.79 | 802.80 ± 34.37 | 285.04 |
| Total consumption (female) | 5412.30 ± 94.51 | 4494.00 ± 140.14 | 3587.80 ± 61.49 | 2620.70 ± 81.27 | 1689.70 ± 61.19 | 905.20 ± 52.48 | 368.30 |

Values are mean ± SE.
* Significant at $P < 0.001$.

Table 3. Different ecological attributes of *Coccinella transversalis* on six aphid species ($n = 10$)

| Aphid species | <i>A. gossypii</i> | <i>A. craccivora</i> | <i>L. erysimi</i> | <i>M. persicae</i> | <i>U. compositae</i> | <i>A. nerii</i> | F-value* |
|-----------------------------------|--------------------|----------------------|-------------------|--------------------|----------------------|-----------------|----------|
| Immature survival (%) | 68.33 | 64.07 | 60.24 | 57.40 | 49.19 | 37.75 | — |
| Growth index | 7.82 | 6.32 | 5.24 | 4.53 | 3.28 | 2.18 | — |
| Adult emergence (%) | 88.21 | 85.98 | 82.39 | 78.86 | 70.96 | 60.69 | — |
| Developmental rate | 0.077 | 0.069 | 0.061 | 0.057 | 0.053 | 0.049 | — |
| Relative growth rate | 0.96 | 0.80 | 0.64 | 0.50 | 0.38 | 0.31 | — |
| Male longevity (in days) | 81.60 ± 1.54 | 74.30 ± 1.93 | 65.50 ± 1.62 | 56.20 ± 1.10 | 46.30 ± 1.42 | 39.70 ± 0.75 | 154.04 |
| Female longevity (in days) | 86.10 ± 0.19 | 79.50 ± 1.51 | 70.80 ± 1.98 | 61.80 ± 1.06 | 51.50 ± 0.82 | 41.90 ± 1.00 | 160.50 |
| Pre-oviposition period (in days) | 9.70 ± 0.34 | 10.30 ± 0.30 | 12.80 ± 0.49 | 13.90 ± 0.28 | 14.60 ± 0.45 | 15.80 ± 0.57 | 33.41 |
| Oviposition period (in days) | 67.80 ± 1.44 | 58.40 ± 1.71 | 46.00 ± 2.13 | 34.30 ± 0.93 | 22.70 ± 1.16 | 11.60 ± 0.69 | 225.10 |
| Post-oviposition period (in days) | 8.50 ± 0.34 | 10.80 ± 0.36 | 12.00 ± 0.54 | 13.60 ± 0.31 | 14.20 ± 0.33 | 15.30 ± 0.78 | 27.87 |
| Fecundity (in eggs) | 1399.60 ± 22.58 | 1155.90 ± 33.18 | 874.00 ± 45.16 | 596.00 ± 22.31 | 366.90 ± 19.24 | 159.40 ± 16.61 | 291.90 |
| Percentage viability in eggs (%) | 92.25 ± 0.78 | 90.84 ± 1.76 | 82.20 ± 1.62 | 78.10 ± 2.98 | 72.22 ± 1.58 | 65.07 ± 1.25 | 38.22 |
| Mean reproductive rate (in eggs) | 20.64 | 19.79 | 19.00 | 17.38 | 16.16 | 13.74 | — |

Values are mean ± SE.
* Significant at $P < 0.001$.

Females weigh heavier than males owing to high relative aphid consumption, resulting in increased fat deposition (DIXON, 2000). Females were relatively larger in size. Earlier, four hypotheses were proposed to explain this size dimorphism amongst the two sexes of ladybeetles. First, it is a consequence of selection for rapid development and early maturation of males, i.e. protandry or development constraint hypothesis (FAIRBAIRN, 1990). Secondly, males begin developing their gonads earlier in their development than females and this has costs in terms of the growth rate that males can sustain, i.e. the gonadal constraint hypothesis (DIXON, 2000). Thirdly, females need to be relatively bigger than males, owing to the direct size dependent fecundity for quantitative progeny production, i.e. the fecundity advantage hypothesis (FAIRBAIRN, 1990). Lastly, in mating systems dominated by scramble for food, small males will be favoured owing to their lesser food requirements and more available time needed in mate searching, i.e. time and energy constraint hypothesis (GHISELIN, 1974; REISS, 1989).

4.2 Larval and adult consumption on six aphids

Prey consumption gradually increased with the age of developing stages, viz. first, second, third and fourth instar larvae, adult male and female. Fourth instar was most voracious amongst different instars. Aphid consumption by different stages of *C. transversalis* increased progressively with the larval growth, owing to increased food requirement for growth and metabolic functions with successive instars. Small sized and slow crawling first instars spent long in prey finding and thus resulted in minimum aphid consumption. Fourth instars consumed largest number of aphids, possibly owing to the increased requirements of food energy for growth (SHARMA et al., 1997) and to attain critical weight for pupation (FERRAN and LARROQUE, 1977). Digestive capacity of larvae may be greater than adults, thus enabling the larvae to consume more aphids (AGARWALA and BARDHANROY, 1997). Fourth instars also detect alarm kairomones of prey more efficiently than adults, which might help them in increased prey capture (NAULT and BOWERS, 1974).

The prey choice is directly linked to prey quality, requirement of high-energy resources for metabolism and reproduction, and to high lipids and proteins (HOUCK, 1991). *Aphis gossypii* is an essential food for *C. transversalis*, which allows faster development and maximum survival. GEORGE (2000) also noticed maximum consumption of *A. gossypii* by the adult *C. transversalis* when compared with aphids, *Pentalonia* sp. and *A. nerii*.

Females consumed more aphids than male ladybeetles, which may be ascribed to their large body sizes and more food requirements for ovarian development, to maintain fertility and to lay eggs (LUCAS et al., 1997). RHAMHALINGHAN (1987) observed that high aphid consumption by females usually occur in their reproductive phase, owing to the high nutrient requirement for the rapid growth of their germ cells. Smaller body size is a reason for lesser aphid consumption by male ladybeetle. Furthermore, males are more active, spend-

ing more time in mate search than in foraging and feeding.

The relative preference might possibly be due to (1) sensory perception prior to consumption and (2) to a prior bad learning experience. It can be said that reduced consumption of such prey might be an adaptive strategy to maintain the unwanted chemicals below harmful levels but still ensure survival, although lower (DIXON, 2000). All the stages of *C. transversalis* consume minimum number of *A. nerii*, which may be listed as a poor essential food, possibly on account of presence of certain alkaloids (EMRICH, 1991) and also its escape efficiency. In the present investigation, it was observed that the individuals of *A. nerii* were relatively more mobile than other aphids and walked away randomly, which hindered the predator in prey capturing. HAJEK and DAHLSTEN (1987) found that long legged aphid, *Eucallipterus betulae* was highly mobile and could escape from the predator's attack, which has led to its relative lesser consumption when compared with other aphid species. KALUSHKOV (1998) observed a neonate larva of *Adalia bipunctata*, while sucking on a much bigger aphid, *Macrosiphoniella artemisiae*, was dragged by the aphid in its attempt to escape from predators. Less consumption of other aphid species may possibly be due to the release of alarm kairomones. The kairomones produced by different aphid species are different and certain kairomones may attract the beetles for feeding, while others may deter feeding (SENGONCA and LIU, 1994).

4.3 Reproduction on different aphid species

The results suggest that reproductive attributes of *C. transversalis* were prey quality dependent. The pre-oviposition period was shortest when females devoured *A. gossypii*. High nutritive content and increased consumption of aphid might accelerate the maturation of the ovarioles, which possibly resulted in the short pre-oviposition period. The post-oviposition period was also shortest on this aphid. Thus, it can be inferred that preferred prey enhanced the reproductive phase, while the consumption of non-preferred food increased the non-reproductive phase.

Relatively high fecundity when the beetles fed on *A. gossypii* may be due to early ovariole ripening, which is prey species dependent, as also opined by RHAMHALINGHAN (1987). The percentage egg viability was also influenced by prey quality. The greater amount of consumption of preferred prey increased the weight of eggs, which contained a large quantity of yolk and consequently increased egg hatching (SIMMONS, 1988). Despite having being provided with aphids of equal wet weights, the relatively high fecundity of the female exposed to *A. gossypii* may be attributed to a probable more efficient prey biomass conversion and allocation (BAUMGÄRTNER et al., 1987).

The presence of various nutrients, viz. free amino acids, proteins, carbohydrates and lipids renders the prey quality more nutritive and essential for the development of the beetles (BABU, 1999). The decreased prey consumption of other aphid species by *C. transversalis* suggests that all aphid species are not

equally suitable and only a few species are suitable for growth and development of the ladybeetles depending upon their biochemical composition. The relatively high longevity of the females than male ladybeetles on different aphid species may possibly be attributed to more prey consumption. This possibly resulted in increased storage food reserves in the female in the form of fat. Thus, the female lived longer. Relatively lesser aphid consumption by males resulted in decreased fat body formation, thereby reducing longevity (Ryoo, 1996). The relatively more kinetic and active life of male beetles, thereby dissipating high energy, might also be responsible for his decreased life-span.

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