Eur. J. Entomol. **111**(3): 363–369, 2014
doi: 10.14411/eje.2014.046
ISSN 1210-5759 (print), 1802-8829 (online)

Stage specific consumption and utilization of aphids, conspecific and heterospecific eggs by two species of *Coccinella* (Coleoptera: Coccinellidae)

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Key words. Coleoptera, Coccinellidae, *Coccinella septempunctata*, *C. transversalis*, conspecific, heterospecific, conversion efficiency, eggs, aphids, *Acyrthosiphon pisum*, consumption rate, growth rate, developmental duration

Abstract. The nutritive quality of aphids, conspecific and heterospecific eggs as food for ladybirds is a controversial issue. If ladybirds find aphids more palatable than eggs then they are more likely to efficiently exploit and be biocontrol agents of aphids. If eggs of conspecific or heterospecific ladybirds are more palatable than aphids these biocontrol agents may either impede aphid pest suppression or become a threat to other species of ladybirds. Thus, prior to formulating predatory guilds of ladybirds the nutritive quality of their eggs compared to that of the target aphid needs to be determined. In this regards, the present study evaluates the nutritive quality of an ad libitum supply of: (i) pea aphid, *Acyrthosiphon pisum* (Harris), (ii) conspecific eggs and (iii) heterospecific eggs as food for *Coccinella septempunctata* (L.) and *Coccinella transversalis* Fabricius (Coleoptera: Coccinellidae), by determining the stage specific predation and developmental attributes of these two ladybirds reared on these diets. The conversion efficiencies and growth rates of young (first, second and third) larvae of both species of ladybirds were higher than those of fourth instar larvae and the consumption rates of fourth instar were higher than those of young larvae when fed on the three diets. When fed aphids the pre-imaginal development was faster, the consumption rates, conversion efficiencies and growth rates higher, adults bigger and mortality lower than when fed on conspecific eggs. The larvae of *C. septempunctata* consumed and completed their development when fed eggs of *C. transversalis* but the first instar larvae of *C. transversalis* did not consume the eggs of *C. septempunctata* and died of starvation. The dominance of *C. septempunctata* over *C. transversalis* in agricultural fields may be due to it consuming and utilizing aphids more efficiently and as a consequence growing faster and suffering a lower mortality along with its ability to consume and complete its development on eggs of *C. transversalis*. Thus, both these predators may not continue to coexist as predators of the pea aphid in agricultural fields since *C. septempunctata* may become a greater threat to *C. transversalis* in the future.

INTRODUCTION

Majority of ladybirds (Coleoptera: Coccinellidae) are generalist predators with wide prey ranges, which include sternorrhynchan Hemiptera, Thysanoptera, phytophagous mites, young instars of holometabolous insects (Evans, 2009) and even fungi (Hodek et al., 2012), which has resulted in their categorization as either aphidophagous, coccidophagous, acarophagous or mycophagous. It is assumed that because they are best at exploiting aphids (Pettersson et al., 2005; Evans, 2008) aphidophagous ladybirds will grow better when feeding on aphids than on non-aphid prey. However, due to their short life span and patchy distribution, the availability of aphids is quite uncertain, which may sometimes result in ladybirds starving in the field. Under such circumstances, cannibalism and intraguild predation (IGP) provide alternative means of sustaining their development and survival (Agarwala & Dixon, 1992; Snyder et al., 2000; Cottrell, 2007). Cannibalism enables larvae to optimally utilize the resources in a patch and IGP results in the dominant species monopolizing the resources and a decrease in the abundance of competitors (Dixon, 2000; Hodek et al., 2012). Thus, both these mechanisms determine the efficiency with which the resources at a specific feeding site are utilized.

In cannibalism, conspecific eggs, larvae, especially neonates and pupae are consumed (Dong & Polis, 1992; Dixon, 2000), while in IGP, vulnerable life stages of other species are consumed (Lucas, 2005; Hemptinne et al., 2011). Of the various stages, eggs are most likely to be attacked by predators, because they are immobile, poorly defended (Agarwala & Dixon, 1992; Felix & Soares, 2004; Michaud & Grant, 2004) and likely to be a high quality food (Gagné et al., 2002; Omkar et al., 2006). Many studies indicate that ladybird larvae fed conspecific (Gagné et al., 2002; Pervez et al., 2006; Roy et al., 2007) or heterospecific eggs (Pilipjuk et al., 1982; Pfannenstiel & Yeargan, 2002; Specty et al., 2003; De Clercq et al., 2005; Michaud & Jyoti, 2008) do better than when fed aphids whereas others indicate that conspecific and/or heterospecific eggs are inferior to aphids as food for ladybird larvae (Koide, 1962; Warren & Tadic, 1967; Takahashi, 1987; Snyder & Clevenger, 2004; Rieder et al., 2008; Sloggett et al., 2009; Sloggett & Davis, 2010). Thus, the relative nutritive value of conspecific eggs, heterospecific eggs and aphids is a controversial issue.

It is suggested that because aphids are generally abundant and palatable, ladybirds prefer to consume them and so behave as biocontrol agents (Hodek et al., 2012) since defen-

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sive surface chemicals deter ladybirds from attacking eggs (Agarwala & Dixon, 1992; Hemptinne et al., 2000a, b). In contrast, the harmful alkaloids that certain aphid species sequester from their host plants render them less suitable prey for ladybirds (Obatake & Suzuki, 1985; Noble et al., 2002) and as a consequence conspecific (Agarwala & Dixon, 1992; Omkar et al., 2006) and heterospecific eggs are more available/palatable prey than aphids for these biocontrol agents and this may either impede aphid pest suppression or pose a threat to other ladybirds (Brown et al., 2011). Therefore, prior to the mass multiplication of ladybirds in laboratories or formulation of predatory guilds of ladybirds for use in the control of aphid pests, a laboratory assessment of the nutritive suitability of the eggs as food for the various ladybirds versus the target aphid is needed. In this regard, the present study evaluates the nutritive suitability of pea aphid, *Acyrthosiphon pisum* (Harris) and eggs of *Coccinella septempunctata* (L.) and *Coccinella transversalis* Fabricius as food for these ladybirds in terms of consumption rate, conversion efficiency and growth rate of their larvae, total duration of development of immature stages, mean body mass of newly emerged adults and percentage larval mortality.

Coccinella septempunctata, though of Palearctic origin, is ubiquitous, with wide tolerance of different climatic conditions and able to forage in wide range of habitats (Hodek & Michaud, 2008; Hodek et al., 2012). It is a large species, prominent in Indian agroecosystems where it is considered to be an indigenous species (Omkar & Bind, 1993; Omkar & Srivastava, 2003). *Coccinella transversalis* is another large species of Oriental ladybird, native to India and found mainly in south Asia (Omkar & Bind, 1993). Both these ladybirds co-exist as predators of numerous species of aphids that infest agricultural crops around Lucknow, India, especially when the aphid colonies are in an early stage of development (Mishra et al., 2012). During the later stages of these aphid colonies, *C. septempunctata* dominates and displaces *C. transversalis* (pers. observ.), but the reasons for this are unknown.

As is evident from earlier studies, ladybirds that are efficient at converting food into their own biomass are also efficient in converting prey biomass into progeny (Omkar et al., 2005). Therefore, evaluating consumption rate, conversion efficiency and growth rate of ladybirds on different diets may also provide information on how they allocate resources to various biological activities (i.e. reproduction and progeny fitness) when fed different diets (Kumar et al., 2013). In this context, the present study: (i) compares the consumption and utilization of aphids, conspecific and heterospecific eggs by the different larval stages of *C. septempunctata* and *C. transversalis*, (ii) identifies the best diet in terms of aphids and eggs for larval growth, development and survival, and (iii) explains the dominance of *C. septempunctata* over *C. transversalis* in terms of their predatory attributes.

MATERIAL AND METHODS

Stock culture

Adults of *C. septempunctata* and *C. transversalis* (n = 50 each) were collected from three agricultural (cereal/ oil crops) and five horticultural (vegetable crops/ pulses) fields close to Lucknow, India (26°50´N, 80°54´E), paired and reared in plastic Petri dishes (14.5 × 1.5 cm^2; diameter × height) under constant abiotic conditions (27 ± 2°C; 65 ± 5% RH; 14L : 10D) in Environmental Test Chambers (ETC; CH-6S Remi Instruments, India). They were fed an ad libitum supply of the aphid, *A. pisum*, which is the most nutritive of the locally abundant aphid species, viz. *Aphis craccivora* Koch, *Aphis gossypii* Glover, *Lipaphis erysimi* (Kaltenbach), *Myzus persicae* (Sulzer) and *Rhopalosiphum maidis* (Fitch) (Omkar et al., 1999; Omkar & Srivastava, 2003; Kumar et al., 2013) infesting broad bean, *Vicia faba* L. (Fabaceae). A stock culture of this aphid was reared on broad-bean plants kept in a polyhouse (22 ± 1°C; 65 ± 5% relative humidity and 14L : 10D photoperiod). Eggs laid by the ladybirds were collected every 24 h and on hatching the neonates were used in the experiment.

Experimental design

Neonates of both *C. septempunctata* (n = 45) and *C. transversalis* (n = 45) were weighed immediately after hatching, using an electronic balance (Sartorius CP225-D; 0.01 mg precision) and then kept individually in Petri dishes (size as above and abiotic conditions similar to those at which the stock culture were kept). They were provided with one of the following diets (n = 15 per diet per ladybird species): (i) ad libitum supply of conspecific eggs, (ii) ad libitum supply of heterospecific eggs (eggs of *C. septempunctata* for *C. transversalis* and vice versa), and (iii) ad libitum supply of third instar pea aphids, *A. pisum.*

Prior to starting the experiments, the ad libitum biomass of the three diets was standardized in terms of the daily food requirement of fourth instar larvae (the most voracious stage; Mishra et al., 2012) of both ladybirds. This indicated that either 75 mg of aphids per day (~ 150 third instar aphids) or 8 mg of eggs per day (~ 100 conspecific/ heterospecific eggs) constituted an ad libitum supply of food for the fourth instar larvae of both species of ladybirds as aphids/ eggs remained unconsumed after 24 h. Although, the daily food requirement of first, second and third instar larvae is lower than that of fourth instar larvae, they were given the same biomass of aphid/ conspecific/ heterospecific eggs as fourth instar larvae. Eggs used in the experiments were non-sibling eggs and less than 24 h old.

The larvae were maintained on these diets throughout their development. The larvae were separated from the remaining biomass of the respective diets every 24 h, which was weighed before providing the larvae with a fresh supply of food. Also the Petri dishes were examined every 24 h for the presence of larval moult skins (indicative of the next developmental stage), and once they moulted the biomass of the larvae was measured. The durations of different larval stages, pre-pupal and pupal periods were recorded on each diet. The mortality of different larval stages fed these diets was also recorded. The observations were made daily, i.e. at 24 h intervals.

To assess the reduction in biomass of eggs and aphids that occurs in absence of ladybird larvae (especially that of aphids, since they were not supplied with pieces of their host plant to feed on), measured amounts of these diets (i.e. 8 mg, 8 mg and 75 mg, respectively) were placed in Petri dishes, which were kept under similar abiotic conditions for 24 h and then weighed. The average loss (if any) in biomass of these diets based on 5 replicates was used to correct the data on consumption prior to calculating the various parameters. Consumption rate, conversion efficiency and growth rate of larvae (per stage) were calculated using the following formulae:

(1) Consumption rate (mg·day^{-1}) (modified after Lucas et al., 2004) equals to:

$$\frac{\text{Aphid/egg biomass (mg) consumed by larval instar}}{\text{Duration (days) of larval instar}}$$

(2) Conversion efficiency (modified after Dixon, 2000) equals to:

$$\frac{\text{Increase in biomass (mg) of larval instar}}{\text{Aphid/egg biomass (mg) consumed by larval instar}}$$

(3) Growth rate (days^{-1}) (modified after Mishra et al., 2012) equals to:

$$\frac{\text{Fresh biomass gain (mg) by larval instar}}{\text{Duration (days) of larval instar} \times \text{Mean body mass (mg) of larval instar}}$$

Statistical analysis

The normality of the distributions of the data obtained in this study were checked using the Kolmogorov-Smirnoff test for normality and Bartlett's test for homogeneity of variances prior to the main analysis.

Consumption rate, conversion efficiency and growth rate of larvae (dependent factors) were individually subjected to repeated measures of analysis of variance (r-ANOVA), followed by Tukey's post hoc comparison of means. Ladybird species (SP), diet (D), larval stage (ST) and their interaction (SP × D × ST) were the independent factors in this analysis. However, when total duration of development of immature stages and mean body mass of newly emerged adults (dependent factors) were individually subjected to r-ANOVA along with Tukey's post hoc comparison of means, ladybird species (SP), diet (D) and their interaction (SP × D) were the independent factors in this analysis.

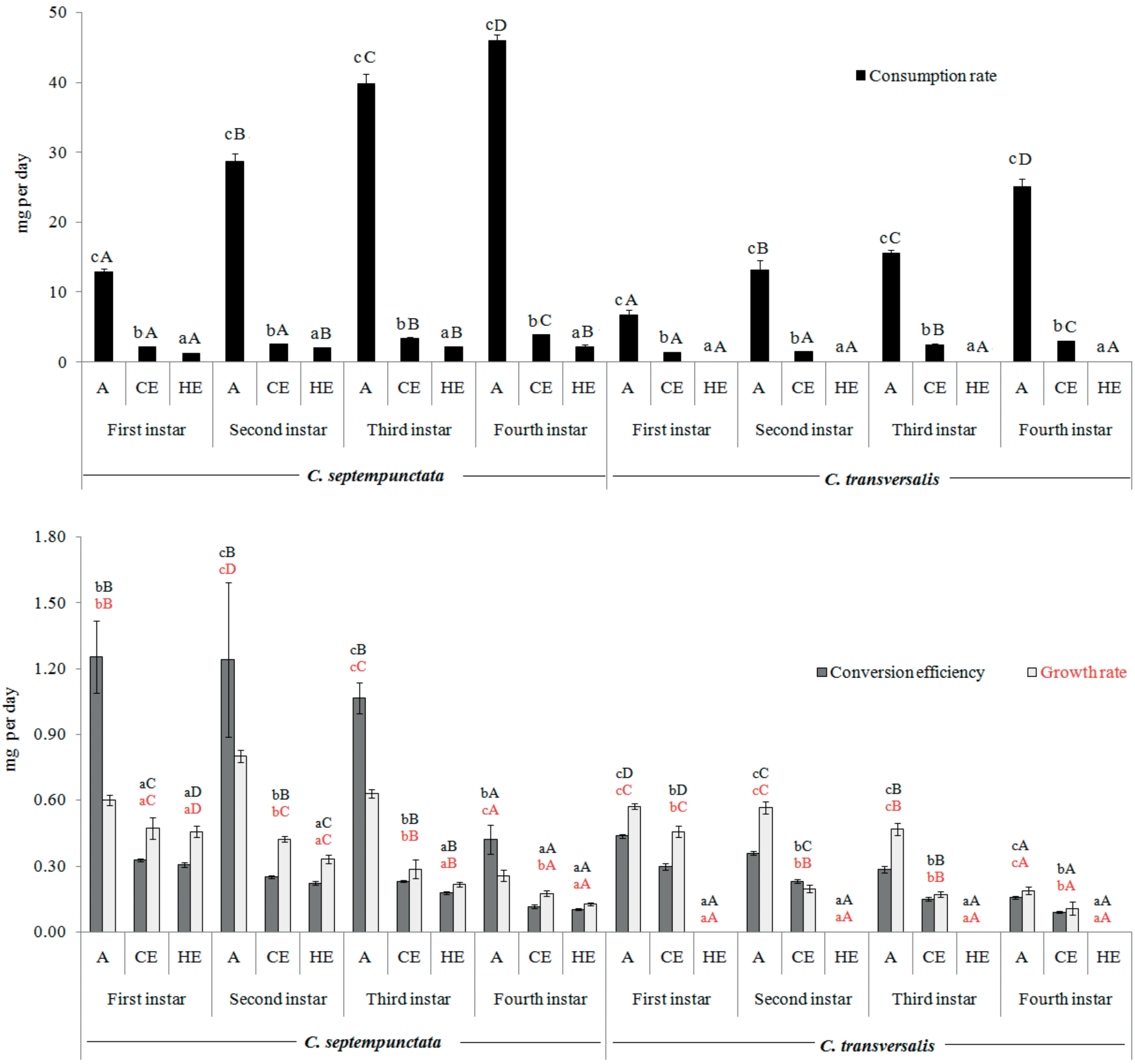

Fig. 1. Effect of diet on the consumption rates, conversion efficiencies and growth rates of larvae of *C. septempunctata* and *C. transversalis* (Values are Means ± SE; A, CE and HE indicate aphid, conspecific and heterospecific egg diets, respectively; small and large letters indicate results of comparison of means among diets and larval instars, respectively; *C. transversalis* did not consume heterospecific eggs).

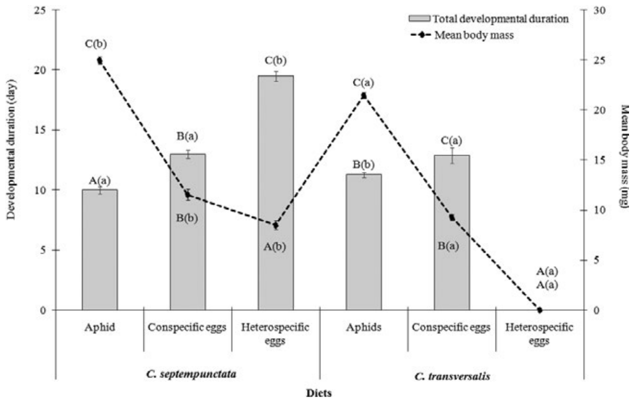

Fig. 2. Effect of diet on total duration of development and mean body mass of newly emerged adults of *C. septempunctata* and *C. transversalis* (Values are Means ± SE; large letters and small letters in parentheses indicate results of comparison of means among diets and between ladybird species, respectively; all the larvae of *C. transversalis* died when fed on heterospecific eggs.

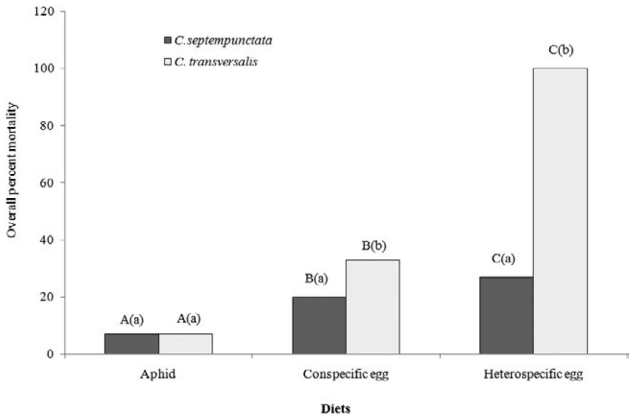

Fig. 3. Effect of diet on the overall percentage mortality of larvae of *C. septempunctata* and *C. transversalis* (large letters and small letters in parentheses indicate the results of the comparison of means among diets and between ladybird species, respectively).

Percentage mortality of larval instars on different diets were subjected to χ^2-test, followed by Tukey's post hoc comparison of means. All statistical analyses were performed using the statistical software SAS (Version 9.0).

RESULTS

Consumption rate of larvae was significantly influenced by the three independent factors, viz. ladybird species, diet and larval stage ($F_{SP \times D \times ST} = 25.68$; $P < 0.0001$; df = 6, 239). Consumption rates of the larval stages of both ladybirds ($F_{ST} = 265.57$; $P < 0.0001$; df = 3, 239) were highest for the fourth instar, followed by the third and second instar and lowest for the first instar. On the three different diets ($F_D = 3099.50$; $P < 0.0001$; df = 2, 239), consumption rate was highest when fed aphids, followed by conspecific eggs and lowest on heterospecific eggs. More of the three diets was consumed by the larvae of *C. septempunctata* than *C. transversalis* ($F_{SP} = 496.12$; $P < 0.0001$; df = 1, 239). Although, *C. septempunctata* consumed the eggs of *C. transversalis* the latter did not consume the eggs of the former and died of starvation (Fig. 1).

Repeated measures ANOVA further revealed significant effects of the three independent factors, viz. ladybird species ($F_{SP} = 25.14$; $P < 0.0001$; df = 1, 239 and $F_{SP} = 20.93$; $P < 0.0001$; df = 1, 239, respectively), diet ($F_D = 67.58$; $P < 0.0001$; df = 2, 239 and $F_D = 204.67$; $P < 0.0001$; df = 2, 239, respectively) and larval stage ($F_{ST} = 4.78$; $P = 0.003$; df = 3, 239 and $F_{ST} = 220.64$; $P < 0.0001$; df = 3, 239, respectively), and their interaction ($F_{SP \times D \times ST} = 4.26$; $P < 0.0001$; df = 6, 239 and $F_{SP \times D \times ST} = 6.50$; $P < 0.0001$; df = 6, 239, respectively) on the conversion efficiency and growth rate of larvae. The conversion efficiencies and growth rates of larvae of both *C. septempunctata* and *C. transversalis* were higher for the early (first, second and third) instars than the fourth instar and higher for the larvae of *C. septempunctata* than *C. transversalis*. On the three diets, conversion efficiency and growth rate were highest on a diet of aphids, followed by conspecific eggs and lowest on heterospecific eggs. The larvae of *C. septempunctata* utilized the three diets more efficiently than *C. transversalis*. Though the larvae of *C. septempunctata* consumed and efficiently utilized the eggs of *C. transversalis* the larvae of the latter did not eat the eggs (heterospecific eggs) of former and died of starvation (Fig. 1).

Further, the total duration of development of immature stages and mean body mass of newly emerged adults were significantly influenced by species of ladybird ($F_{SP} = 4.34$; $P = 0.042$; df = 1, 59 and $F_{SP} = 96.71$; $P < 0.0001$; df = 1, 59, respectively), three different diets ($F_D = 299.40$; $P < 0.0001$; df = 2, 59 and $F_D = 1701.17$; $P < 0.0001$; df = 2, 59, respectively) and their interaction ($F_{SP \times D} = 4.34$; $P = 0.018$; df = 2, 59 and $F_{SP \times D} = 8.47$; $P = 0.001$; df = 2, 59, respectively). The total duration of development of the immature stages was shortest and newly emerged adults heaviest when both ladybirds were fed on aphids. In contrast, when fed on heterospecific eggs, the duration of development of the immature stages of *C. septempunctata* was longer and newly emerged adults were lighter, whereas the first instar of *C. transversalis* did not eat the heterospecific eggs and died of starvation. The total duration of development of the larvae of *C. septempunctata* was shorter/slightly shorter and newly emerged adults heavier than those of *C. transversalis* (Fig. 2) when reared on a diet of aphids or conspecific eggs.

The percentage mortality of the larvae of both *C. septempunctata* ($\chi^2 = 11.67$; $P = 0.003$; df = 2) and *C. transversalis* ($\chi^2 = 99.05$; $P < 0.0001$; df = 2) differed significantly on the three diets, with the highest mortality recorded when they were fed heterospecific eggs, followed by conspecific eggs, and lowest when fed aphids. The same percentage larval mortality was recorded for both *C. septempunctata* (7%) and *C. transversalis* (7%) when they were fed aphids. However, when fed conspecific and heterospecific eggs the percentage mortality of the larvae of *C. transversalis* (33% and 100%, respectively) was higher than that of the larvae of *C. septempunctata* (20% and 27%, respectively) (Fig. 3).

DISCUSSION

In the present study the fourth instar larvae of both *C. septempunctata* and *C. transversalis* had higher consumption rates than the early instars on the three diets. In contrast, the early instars had higher conversion efficiencies and growth rates than the fourth instar. In addition, consumption rates, conversion efficiencies and growth rates of larvae were highest when they were fed aphids, followed by conspecific eggs. The consumption rate, conversion efficiency and growth rate of larvae of *C. septempunctata* were lowest when they were fed heterospecific eggs and the neonates of *C. transversalis* did not eat heterospecific eggs and died.

That the consumption rate of fourth instar larvae was higher than that of the earlier instars on the three diets is possibly because they are larger, have a higher energy requirement (Ahlawat et al., 2008; Finlayson et al., 2010; Mishra et al., 2012) and store energy for future development and metamorphosis (Ferran & Larroque, 1977; Isikber & Copland, 2001). In contrast, the higher conversion efficiencies and growth rates of earlier instars compared to fourth instar larvae may be attributed to their small size, low metabolic costs and low energy needs (Isikber & Copland, 2001; Jalali et al., 2009; Mishra et al., 2012).

Perhaps, the larvae of *C. septempunctata* consumed and utilized the different diets more efficiently than *C. transversalis* because the larvae of *C. septempunctata* are more polyphagous and ecologically plastic (intrinsic advantages) (Hodek & Michaud, 2008). The higher consumption and growth rates recorded for larvae of *C. septempunctata* than those of *C. transversalis* when fed pea aphids have been reported previously (Mishra et al., 2012).

That the highest consumption rates, conversion efficiencies and growth rates of larvae of both the ladybirds were recorded on an aphid diet further indicate that aphids possibly contain better and more essential nutrients than conspecific or heterospecific eggs. As the three parameters recorded are regulated by the nutrients in food items (Isikber & Copland, 2001; Hodek et al., 2012) this further indicates that highly nutritious prey is consumed and assimilated faster. Females of *Harmonia axyridis* (Pallas) consume and assimilate the highly nutritious pea aphid, *A. pisum,* more quickly than the less nutritious larvae of alfalfa weevil, *Hypera postica* (Gyllenhal) (Evans & Gunther, 2005). The present findings are also in agreement with many earlier studies on ladybirds (Koide, 1962; Warren & Tadic, 1967; Takahashi, 1987). Moreover, as predators prefer mobile prey the mobility of aphids may also result in more of them being consumed (Eubanks & Denno, 2000; Prabhakar & Roy, 2010).

In contrast, eggs are immobile and their defensive surface semiochemicals, which are rich in alkanes and alkaloids (Hemptinne et al., 2000a, b; Omkar et al., 2004), reduce their consumption and utilization by larvae. However, the chemicals on the surface (alkanes) and within eggs (alkaloids) attract conspecifics (Pasteels et al., 1973; Dixon, 2000) and provide protection against heterospecifics (Rieder et al., 2008; Ware et al., 2009), which resulted in conspecific eggs being consumed and utilized more than heterospecific eggs in the present study. There are similar earlier findings reported for other ladybirds (Hemptinne et al., 2000a, b; Omkar et al., 2004; Rieder et al., 2008; Ware et al., 2009).

The present study further revealed that when reared on a diet of aphids both ladybirds took less time to complete their development and were bigger than those fed on conspecific/heterospecific eggs. The greater consumption rates recorded when they were fed aphids may be because they are more palatable than ladybirds' eggs (Koide, 1962; Warren & Tadic, 1967; Takahashi, 1987). In addition, the ladybirds studied may utilize the nutrients in aphids with greater efficiency than those in con- or heterospecific eggs, which could also result in larvae taking less time to develop and bigger adults. The results are in agreement with many previous studies (Sato & Dixon, 2004; Cottrell, 2007; Sloggett et al., 2009; Kajita et al., 2010; Hemptinne et al., 2011). Further, because of its higher consumption rates, conversion efficiencies and growth rates the immature stages of *C. septempunctata* developed faster and the adults were bigger when fed on aphid or eggs than were those of *C. transversalis*.

The lower consumption, conversion and utilization, slow development of larvae and reduced body mass of adults at emergence when reared on eggs rather than aphids recorded in the present study indicate that eggs may be an alternative food for the larvae of these ladybirds when food is scarce. However, the present findings differ from those of many earlier studies that report a better performance of larvae reared on eggs than on aphids (Agarwala, 1991; Agarwala & Dixon, 1993).

In the present study, larvae of *C. septempunctata* completed their development, although more slowly, when fed heterospecific eggs (i.e. *C. transversalis* eggs). In contrast, neonates of *C. transversalis* did not consume the eggs of *C. septempunctata*. Although the eggs of both ladybirds were not analyzed chemically/biochemically in the present study it is possible that the defensive alkanes/alkaloids on the surface of *C. transversalis* eggs are either less toxic to *C. septempunctata* larvae or they are able to consume, detoxify and metabolize these eggs. However, the surface chemicals of heterospecific eggs are possibly less palatable than those of conspecific eggs, as the larvae of *C. septempunctata* consumed fewer eggs of *C. transversalis* than of its own eggs. In contrast, the egg surface chemicals of *C. septempunctata* are probably toxic and cannot be detoxified and assimilated by neonates of *C. transversalis*. Therefore, the neonates of *C. transversalis* did not consume the eggs of *C. septempunctata* in the present study and died of starvation.

In brief, owing to its aggressive nature, ability to displace co-existing ladybirds (viz. *Coccinella transversoguttata* Brown, *Hippodamia convergens* Guerin-Meneville, *Adalia bipunctata* L., *Coccinella novemnotata* Herbst (Wheeler & Hoebeke, 1995; Elliott et al., 1996; Snyder et al., 2004)) and high tendency to attack *C. transversalis* (Gupta et al., 2006), larvae of *C. septempunctata* dominate *C. transver-*

salis in agricultural fields. Other possible reasons for the dominance of *C. septempunctata* revealed by the present study, are: (i) its higher consumption, and conversion of prey biomass into its own biomass, (ii) its ability to consume and complete its development on a diet of eggs of *C. transversalis*, and (iii) its lower percentage mortality when fed on conspecific and heterospecific eggs than that of *C. transversalis*. Therefore, releasing both predators together to control populations of pea aphids in the field is risky, since *C. septempunctata* may become a threat to *C. transversalis* once the pea aphids are controlled. However, future studies should: (i) compare the chemical/biochemical nature of the eggs of both these ladybirds, and (ii) assess their fitness, mortality and life table parameters when fed the three experimental diets.

ACKNOWLEDGEMENTS. The authors thank the Department of Higher Education, Government of Uttar Pradesh, India for providing financial assistance in the form of Centre of Excellence in Biocontrol of Insect Pests.

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Received November 25, 2013; revised and accepted February 12, 2014
Prepublished online May 6, 2014