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EVALUATION OF PREDATION AND DEVELOPMENTAL ATTRIBUTES OF TWO CONGENERIC LADYBIRD BEETLES UNDER VARIABLE SUPPLY OF PEA APHID

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Abstract: *Food relations of ladybird beetles are the most investigated aspects of 'coccinellid ecology' because of their obvious role as natural enemies of agricultural pests, viz. aphids, coccids and mites. In agroecosystems, the availability of aphid prey frequently fluctuates in space and time; and its deprivation severely affects the life attributes of ladybird predators. As a result, predatory responses of ladybird species differ under variable quantities of prey. In this regards, the present study has been designed to assess and compare the prey consumption and utilization abilities of two aphidophagous ladybird beetles, i.e. Coccinella septempunctata (L.) and Coccinella transversalis Fab., under scarce, optimal and abundant supply of the pea aphid, Acyrthosiphon pisum (Harris). Results revealed that in both the ladybird species, consumption rates of the fourth instars were higher than the early instars; while conversion efficiencies and growth rates of the early instars were higher than the fourth instars when larvae were fed on the three prey quantities. However, the predation attributes of larvae were highest on the abundant prey and lowest on the scarce prey. Further, the immature stages of both the ladybird species developed fastest and their newly emerged adults were heaviest when larvae were reared on the abundant prey. In contrast, the development of larvae was slowest and newly emerged adults were lightest on the scarce prey supply. These comparative findings will not only improve our understandings of the predation biology and nutritional ecology of these ladybirds, but may also be utilized for augmentative biocontrol of aphid pests.*

Keywords: *Consumption rate, conversion efficiency, growth rate, ladybirds, aphid*

Introduction: In insects, the prey-predator relationship, especially involving the aphids and the ladybird beetles, has been well investigated. Since aphid availability in the agro ecosystem often fluctuates in space and time, its deprivation severely affects the life attributes of ladybirds [1-3]. As a result, predatory responses of ladybird species differ under variable quantities of prey. Such variations in predatory behaviour of ladybirds govern complex interactions (e.g. intra- and inter-specific competitions) between them when preying on a common prey resource [4-5]. Therefore, investigation on intensity and nature of such interactions between ladybird predators in relation to prey scarcity or abundance is of great relevance as they may affect structure of predatory guilds.

The quantity of prey intake, its digestibility and utilization significantly influences the growth, developmental time, final body biomass and survivability of ladybirds [6]. Increased prey consumption by the ladybird [7], *Scymnus subvillosus* (Goeze) with increase in prey density has been previously reported. Similar results were also obtained in ladybird, *Stethorus tridens* [8], and in predaceous mite, *Amblyseius herbicolus* (Chant) [9]. Increased prey consumption by other ladybird beetles with increase in prey density has also been reported earlier [10-13].

Studies have further shown that the larvae of the ladybird, *Harmonia axyridis* (Pallas) compensated for earlier prey shortages by accelerating their growth rates [14]. On limited prey supply, adults of *H. axyridis* had reduced efficiency of converting prey biomass into eggs in comparison to adults provided abundant prey supply [15]. However, reduced prey supply slowed down development at all life stages was also reported [16]. Studies have also shown that reduced rates of prey consumption result in slower development and greater mortality for both larvae and adults [2].

Thus, prey deprivation severely affects the development and survival of ladybirds [17, 18, 13, 16,]. It is believed that under prey scarce conditions the entire energy resources are utilized to maximize the survival and reproduction [19]. Thus, prey scarcity can affect fitness of adults by influencing developmental rate and final size of offspring [20, 18, 21]. In contrast, the developmental durations of larval instars of ladybird beetles became short and their mortality rates were reduced when prey was present in abundance [7, 22].

Because the quantity of prey consumed affects development, survival and reproduction of predators [23-28], one must study predator responses to these factors to understand their ecology including their foraging efficiency and prey consumption. Since performance of both larval and adult predators is constrained by the quantity of prey available [29, 26, 30, 31, 32, 21], this is a very important factor in understanding the fate of predatory insects. Thus, in the present study, the prey consumption and utilization abilities of two ladybird predators, *i.e. C. septempunctata* and *C. transversalis*, have been assessed and compared under scarce, optimal and abundant supply of the pea aphid, *A. pisum*.

Coccinella septempunctata, is of Palearctic origin and is now ubiquitous owing to its euryphagous nature, large size, ability to temporarily cease reproducing, heterogenous voltinism and tendency to enter diapause, absence of reproductive diapause in males, pre-hibernation mating, storage of sperm by females during winter and ecological plasticity in terms of both genetic and phenotypic polymorphism [33]. *Coccinella transversalis* is also a large aphidophagous lady beetle of the Oriental region, native to India and found mainly in South Asia [34]. Both these lady beetles co-exist as predators of the numerous species of aphids that infest agricultural crops grown around Lucknow, India. Because they are polyphagous in the field, both lady beetles are recognized as effective biocontrol agents and used in aphid management programs.

Materials and Methods

Stock Maintenance: Adults of *C. septempunctata* and *C. transversalis* (n = 40) collected from the fields of Lucknow, India (26º50’N, 80º54’E), were paired and reared for three generations in plastic Petri dishes (14.5 × 1.5 cm^2) under constant abiotic conditions (27±2°C; 65±5% RH; 14:10 LD) in BOD incubators (Yorco Super Deluxe, YSI-440, New Delhi, India). They were provided with *ad libitum* aphid, *A. pisum* reared on broad bean, *Vicia faba* L. (Fabaceae) and maintained in polyhouse (22 ± 1ºC; 65 ± 5 % RH and 14L: 10D photoperiod). Wild ladybirds from the fields were frequently added to this established stock to prevent inbreeding. The eggs laid were collected every 24 h, kept in BOD incubators, observed for hatching and the neonates/ requisite stages obtained were used in the experiments.

Experimental Design: Neonates of *C. septempunctata* and *C. transversalis* were weighed 12 h after hatching using an electronic balance (Sartorius CP225-D; 0.01 mg precision) and kept individually in Petri dishes (size as above and abiotic conditions similar to stock), on one of the following diets, *i.e.* (i) scarce prey (25 mg *A. pisum*), (ii) optimal prey (50 mg *A. pisum*), and (iii) abundant prey (75 mg *A. pisum*). The immature stages were maintained on these diets throughout the larval period.

The biomass of the prey was standardized (based on food requirements of third and fourth larval instars) prior to the experimentation to obtain scarce (25 mg), optimal (50 mg) or abundant (75 mg) prey conditions. When fed on scarce prey no aphid was left after 24 h, whereas under optimal prey condition, third/ fourth instars left negligible (< 1.00 mg) aphid biomass in Petri dishes and under abundant prey supply the third/ fourth instars left surplus (4.00±1.00 mg) aphid biomass after 24 h. The stages were separated from the remaining biomass of respective diets every 24 h, which were then weighed and a fresh amount provided. The immature stages were weighed 6 h after each moulting. The durations of different immature stages were recorded on each diet. The observations were made once daily, *i.e.* at 24 h intervals. To assess the reduction in biomass of different diets in absence of a predator (control), measured amounts of these diets were placed individually in Petri dishes, 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 taken into account in the statistical analyses of the data. Consumption rate, conversion efficiency and growth rate of larvae (per stage) were calculated using the following formulae :

1. Consumption rate (mg-day^{-1})[35]

$$= \frac{\text{Aphid biomass (mg) consumed by the larval instar}}{\text{duration (days) of the larval instar}}$$

1. Conversion efficiency [36]

$$= \frac{\text{Increase in predator biomass (mg) with subsequent stage}}{\text{Aphid biomass (mg) consumed during that stage}}$$

2. Growth rate (day^{1}) [37-38]

$$= \frac{\text{Fresh mass gain (mg) of larval instar}}{\text{Duration (days) of larval instar} \times \text{Mean fresh mass (mg) of larval instar}}$$

Statistical Analysis: The data were checked for normal distribution using Kolmogorov-Smirnoff test for normality and Bartlett's test for homogeneity of variances prior to further analysis. Predation parameters, *viz*. conversion efficiency and growth rate (dependent factors), were subjected to three-way ANOVA followed by Tukey's post hoc comparison of means, considering ladybird species, stage, prey quantity and their interactions as independent factors during the analysis.

Total developmental duration of immature stages and mean body mass of newly emerged adults were subjected to two-way ANOVA with ladybird species, prey quantity and their interaction as independent factors, followed by Tukey's post hoc comparison of means. However, consumption rate (dependent factor) was subjected to three-way analysis of covariance (ANCOVA), with ladybird species, stage, prey quantity and their interactions as independent factors and mean body mass as a covariate (general linear model), to neutralize the effect of variable sizes of predatory ladybirds. All statistical analyses were performed on MINITAB 16 (Minitab Inc., State College, Pennsylvania, USA).

Results

(a) Predation Attributes: In the present study, ANCOVA revealed significant influence of mean body mass of larval instars (covariate; F=2.37; P=0.015; df=1, 239), ladybird species (F=42.19; P<0.0001; df=1, 239), prey quantity (F=235.63; P<0.0001; df=2, 239) and larval stage (F=56.74; P<0.0001; df=3, 239) on the consumption rate of larval instars. Although, the interactions between ladybird species and prey quantity (F=7.30; P=0.001; df=2, 239), and between prey quantity and larval stage (F=9.33; P<0.0001; df=6, 239) differed significantly, but the interaction between ladybird species and larval stage (F=1.27; P=0.285; df=3, 239) was insignificant for the consumption rate. In both the ladybird species, highest consumption rate was recorded for the fourth instars on abundant prey and lowest for the first instars on scarce prey supply. Moreover, the consumption rate was recorded higher for *C. septempunctata* than *C. transversalis* (Table 1).

Table-1: Effect of prey quantity on consumption rate, conversion efficiency and growth rate of larval instars of *C. septempunctata* and *C. transversalis*.

Ladybird species	Prey quantity	Larval stage	Consumption rate (mg day^{-1})	Conversion efficiency	Growth rate (per day)
C. septempunctata	**Scarce**	First instars	$5.82\pm0.65^{aA(b)}$	$0.09\pm0.02^{aA(a)}$	$0.40\pm0.10^{bA(a)}$
		Second instars	$15.47\pm0.63^{bA(b)}$	$0.15\pm0.01^{bA(b)}$	$0.48\pm0.12^{bA(a)}$
		Third instars	$19.91\pm0.72^{cA(b)}$	$0.09\pm0.02^{aA(a)}$	$0.53\pm0.03^{bA(b)}$
		Fourth instars	$23.22\pm2.77^{dA(b)}$	$0.06\pm0.01^{aA(a)}$	$0.07\pm0.01^{aA(a)}$
	Optimal	First instars	$7.43\pm0.25^{aB(b)}$	$0.09\pm0.01^{aA(a)}$	$0.77\pm0.06^{cB(b)}$
		Second instars	$17.27\pm1.19^{bB(b)}$	$0.21\pm0.01^{dB(a)}$	$1.17\pm0.04^{dB(a)}$
		Third instars	$24.18\pm0.59^{cB(b)}$	$0.11\pm0.01^{bA(a)}$	$0.61\pm0.06^{bA(a)}$
		Fourth instars	$27.60\pm0.58^{dB(b)}$	$0.14\pm0.00^{cB(b)}$	$0.40\pm0.02^{aB(b)}$
	Abundant	First instars	$26.41\pm1.96^{aC(b)}$	$0.17\pm0.01^{aB(b)}$	$1.03\pm0.07^{bC(a)}$
		Second instars	$47.14\pm5.06^{bC(b)}$	$0.23\pm0.02^{bB(a)}$	$1.34\pm0.04^{cC(b)}$
		Third instars	$54.48\pm3.84^{cC(b)}$	$0.27\pm0.02^{bB(a)}$	$0.88\pm0.06^{bB(b)}$
		Fourth instars	$56.98\pm2.14^{cC(b)}$	$0.15\pm0.02^{aB(a)}$	$0.49\pm0.03^{aC(b)}$
C. transversalis	**Scarce**	First instars	$4.78\pm0.49^{aA(a)}$	$0.08\pm0.01^{bA(a)}$	$0.30\pm0.06^{bA(a)}$
		Second instars	$10.14\pm1.33^{bA(a)}$	$0.12\pm0.01^{cA(a)}$	$0.39\pm0.06^{bA(a)}$
		Third instars	$13.05\pm0.53^{cA(a)}$	$0.08\pm0.01^{bA(a)}$	$0.46\pm0.03^{cA(a)}$
		Fourth instars	$18.32\pm1.35^{dA(a)}$	$0.05\pm0.01^{aA(a)}$	$0.05\pm0.03^{aA(a)}$

Optimal	First instars	5.16±0.55$^{aB(a)}$	0.09±0.01$^{aA(a)}$	0.59±0.08$^{bB(a)}$
	Second instars	12.83±0.24$^{bB(a)}$	0.25±0.04$^{bB(a)}$	1.25±0.12$^{cC(a)}$
	Third instars	15.58±0.26$^{cB(a)}$	0.30±0.04$^{bB(b)}$	0.73±0.13$^{bB(a)}$
	Fourth instars	22.13±0.39$^{dB(a)}$	0.10±0.02$^{aB(a)}$	0.21±0.02$^{aB(a)}$
Abundant	First instars	15.91±0.41$^{aC(a)}$	0.09±0.01$^{aA(a)}$	0.70±0.08$^{bC(a)}$
	Second instars	37.50±3.44$^{bC(a)}$	0.23±0.01$^{cB(a)}$	0.95±0.05$^{cB(a)}$
	Third instars	42.80±1.70$^{cC(a)}$	0.32±0.01$^{dB(b)}$	0.69±0.07$^{bB(a)}$
	Fourth instars	46.95±2.51$^{dC(a)}$	0.14±0.01$^{bC(a)}$	0.30±0.02$^{aC(a)}$

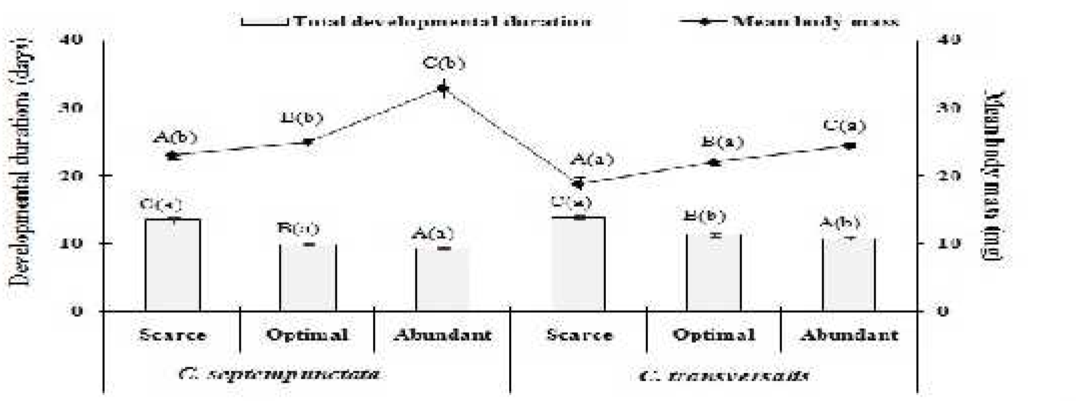
Values are Mean±SE; F-values significant at P<0.05.
Small letters, large letters and small letters in parentheses represent comparison of means among larval stages, among prey quantities and between ladybird species, respectively.

The results of three-way ANOVA revealed that the conversion efficiency of larval instars was significantly influenced by the prey quantity (F=12.73; P<0.0001; df=2, 239) and the larval stage (F=208.14; P<0.0001; df=3, 239). However, the influence of ladybird species on conversion efficiency was not significant (F=1.49; P=0.224; df=1, 239). The interactions between ladybird species and prey quantity (F=0.52; P=0.595; df=2, 239) and between prey quantity and larval stage (F=1.87; P=0.088; df=6, 239) did not differ significantly for the conversion efficiency of larval instars; but the interaction between ladybird species and larval stage (F=4.58; P=0.004; df=3, 239) was significant. In both the ladybird species, conversion efficiency of larval instars was higher on abundant prey than on optimal or scarce prey. Moreover, on the three prey quantities, conversion efficiency was higher for the early instars and lower for the fourth instar (Table 1).

The results of three-way ANOVA further revealed that the growth rate of larval instars was influenced significantly by the prey quantity (F=12.05; P<0.0001; df=2, 239), larval stage (F=145.92; P<0.0001; df=3, 239) and the ladybird species (F=13.02; P<0.0001; df=1, 239). Although, the interaction between ladybird species and prey quantity (F=0.01; P=0.988; df=2, 239) was insignificant; but the interactions between ladybird species and larval stage (F=19.23; P<0.0001; df=3, 239) and between prey quantity and larval stage (F=2.38; P=0.030; df=6, 239) were significant. The growth rate of larval instars of both the ladybird species was highest on abundant prey supply and lowest on scarce prey supply; being higher for the early instars than the fourth instars. Moreover, the growth rate was recorded higher for *C. septempunctata* than *C. transversalis* (Table 1).

(b) Development: The total developmental duration of immature stages differed significantly with the ladybird species (F=6.48; P=0.014; df=1, 59) and the prey quantity (F=42.60; P<0.0001; df=2, 59), but not with their interaction (F=2.06; P=0.138; df=2, 59). The immature stages of *C. septempunctata* developed fastest when fed on abundant prey, whereas those of *C. transversalis* developed slowest under scarce prey supply (Figure 1)

Figure-1: Effect of prey quantity on total developmental duration of immature stages and mean body mass of newly emerged adults of *C. septempunctata* and *C. transversalis*.



Values are Mean±SE.
Small letters and small letters in parentheses represent comparison of means among larval stages and between ladybird species, respectively.

The biomass of newly emerged adults was influenced significantly by the ladybird species (F=112.31; P<0.0001; df=1, 59) and the prey quantity (F=25.65; P<0.0001; df=2, 59), but not by their interaction (F=1.12; P=0.333; df=2, 59). Newly emerged adults of *C. septempunctata* and *C. transversalis* were heaviest when larvae were reared on abundant prey supply and lightest when the larvae were reared on scarce prey supply (Figure-1).

Discussion

In the present study, highest consumption rate, conversion efficiency and growth rate of larval instars, and shortest total developmental duration of immature stages of *C. septempunctata* and *C. transversalis* were recorded on abundant prey; while the reverse were true on the scarce prey supply. Also on the three prey quantity provided: (i) fourth instars had higher consumption rates than the early instars, and (ii) early instars had higher conversion efficiency and growth rate than the fourth instars.

The higher larval consumption rate of both the ladybirds on abundant prey reveals that possibly the abundant prey facilitates larval feeding; as a result the larvae consume more prey than their usual predation rates. Contrary to it, the scarce prey condition constrains the larval feeding capacity, owing to non availability of sufficient food, on account of which they consume less prey than their usual predation rates.

Amongst the larval instars, the present study has revealed higher consumption rates of fourth instars on the given three prey quantities. Higher consumption rate of fourth instars may possibly be attributed to their large size, increased metabolic costs and the need to store more energy for pupation and further metamorphosis. Their higher prey searching efficiency also expedites their consumption rates. In contrast, the lower consumption rates of early instars may be ascribed to their small size, low prey searching efficiency, less energy requirements and low metabolic costs.

In the present study, the higher conversion efficiency of larvae on abundant prey reveals that possibly the abundant prey availability allows the larvae to consume and utilize the prey biomass to their own biomass maximally. In contrast, under the scarce prey conditions, the larvae consume less prey owing to the shortage, which reduces their conversion efficiency. However, the larval stages have shown the comparable conversion efficiencies on scarce prey as on the optimal prey supply despite lowest prey consumption. This suggests that the food conversion efficiency increases under adverse prey conditions so as to reduce the adverse effects of food shortage; but this increase in conversion efficiency on scarce prey supply is still lower than those recorded on abundant prey supply. The findings are in conformity with reports of earlier studies in ladybirds [39, 16, 14]. Similar increased conversion efficiencies at low levels of food consumption were also reported in aphidophagous mirids and chrysopids [40, 24].

The higher conversion efficiencies of early instars may be owing to their small size and low energy requirements. Contrary to them, the fourth instars are large in size, have higher metabolic costs and energy requirements associated with pupation and subsequent metamorphosis. They therefore cannot convert the prey biomass maximally to their own biomass that reduces their conversion efficiencies. Similar findings were also reported earlier [41, 42, 43, 6, 44, 45].

The higher growth rates of larvae on abundant prey, as revealed from the present study, may possibly be due to their higher consumption rates and conversion efficiencies that are responsible for their higher prey consumption, conversion and utilization resulting in their higher growth rates. Also, the higher growth rates of early instars over the fourth instars on the three prey quantities may be attributed to their small size, lower metabolic costs and low energy requirements. In contrast, the fourth instars have reduced abilities in converting the prey biomass to their own biomass, possibly owing to their large size and greater metabolic costs. Thus, they have lower growth rates than the early instars. The decrease in growth rate from early to late instars has also been reported earlier [46, 6].

Shortest developmental duration of immature stages of both C. *septempunctata* and *C. transversalis* after feeding on abundant prey and longest on scarce prey exemplify that some minimum amount of energy is required by each larval stage to develop into the next stage which is regulated by the suitable prey quantity. Studies have shown that the larvae during their latter stages of development require greater amount of food for their growth and attainment of critical biomass for pupation [47, 48, 49] and this requirement is fulfilled under abundant prey supply. In contrast, the slowing down of larval development under prey scarce conditions may be ascribed to the decreased availability of nutrients that results in delayed moulting/ pupation. The findings further suggest that the immature stages of ladybirds probably need higher amount of prey to attain higher predation attributes and developmental rate than the prey available to them under scarce prey supply. Slowing down of larval development during food scarce condition may possibly be a mechanism displayed by larvae to compensate for a lack of food. Similar results have also been reported by the earlier studies [50, 18, 51, 16, 52, 15, 7, 27]. Reduced rates of prey consumption under scarce prey supply, resulting in slower growth and development of ladybird larvae are in conformity with earlier reports [39, 53, 54, 55, 56, 2, 57].

Heavy adults emerged when larval instars were fed on abundant prey. This may be attributed to the higher consumption rates, conversion efficiencies and growth rates of larval instars under abundant prey conditions. In contrast, decreased mean body mass of newly emerged adults on scarce prey supply recorded may be ascribed to the reduced prey consumption by larval instars due to prey shortage.

Results, therefore, reveal that: (i) the predation parameters of larval instars were highest, total developmental durations of immature stages were shortest and mean body mass of newly emerged adults was maximum on abundant prey supply, (ii) early instars had higher conversion efficiency and growth rate, and (iii) fourth instars had highest consumption rates on all prey supply conditions.

The present study suggests that under laboratory conditions, ladybirds perform best when fed on abundant prey, in terms of prey consumption and utilization. But field based studies are still lacking that can evaluate the predatory performance of predators within guilds on scarce, optimal and abundant prey conditions and further validate the laboratory findings. Also, when given a choice of either abundant or optimal prey, the larvae reared on scarce prey showed similar functional response or predatory interactions on these prey as on scarce prey, and *vice versa*? Under high selection pressure due to prey scarcity or deprivation, whether the predation behaviour of larvae remains the same as under optimal or abundant prey condition or are there any deviations/ modifications? The future studies may be designed targeting such questions.

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Conflict of interest

All authors have no potential conflict of interest in relation to this article.

References

1. Omkar & James, B.E. (2003). Searching and feeding efficiency of *Coccinella transversalis* Fabricius on aphid, *Aphis gossypii* Glover. *Journal of Biological Control*, 17(2): 107-112.
2. Phoofolo, M.W., Giles, K.L. & Elliott, N.C. (2008). Larval life history responses to food deprivation in three species of predatory lady beetles (Coleoptera: Coccinellidae). *Environmental Entomology*, 37: 315-322.
3. Santos-Cividanes, T.M., Dos Anjos, A.C.R., Cividanes, F.J. & Dias, P.C. (2011). Effects of food deprivation on the development of *Coleomegilla maculata* (De Geer) (Coleoptera: Coccinellidae). *Neotropical Entomology*, 40 (1): dx.doi.org/10.1590/ S1519566X2011000100 017.
4. Sato, S., Shinya, K., Yasuda, H., Kindlmann, P. & Dixon, A.F.G. (2009a). Effects of intra and interspecific interactions on the survival of two predatory ladybirds (Coleoptera: Coccinellidae) in relation to prey abundance. *Applied Entomology and Zoology*, 44: 215-221.
5. Sato, S., Yasuda, H., Evans, E.W. & Dixon, A.F.G. (2009b). Vulnerability of larvae of two species of aphidophagous ladybirds, *Adalia bipunctata* Linnaeus and *Harmonia axyridis* Pallas, to cannibalism and intraguild predation. *Entomological Science*, 12: 111-115.
6. Rath, S.S. (2010). Food utilization efficiency in *Antheraea mylitta* fed on *Terminalia arjuna* leaves. *Academic Journal of Entomology*, 3(1): 23-28.
7. Atlihan, R. & Guldal, H. (2009). Prey density-dependent feeding activity and life history of *Scymnus subvillosus*. *Phytoparasitica*, 37: 35-41.
8. Britto, E.P.J, Gondim, M.G.C., Torres, J.B., Fiaboe, K.K.M., Moraes, G.J. & Knapp, M. (2009). Predation and reproductive output of the ladybird beetle *Stethorus tridens* preying on tomato red spider mite *Tetranychus evansi*. *BioControl*, 54: 363-368.
9. Reis, P.R., Teodoro, A.V., Neto, M.P. & Da Silva, E.A. (2007). Life history of *Amblyseius herbicolus* (Chant) (Acari: Phytoseiidae) on coffee plants. *Neotropical Entomology*, 36(2): 282-287.
10. Omkar & Srivastava, S. (2001). Comparative predatory potential of a ladybird beetle, *Coccinella septempunctata* Linn. on six prey species. *Biological Memoirs*, 27(2): 59-63.
11. Omkar & Srivastava, S. (2003). Comparative prey consumption and searching efficiency of

ladybeetles, *Coccinella septempunctata* Linnaeus and *Coccinella transversalis* Fabricius for different aphid species. *Journal of Biological Control*, 17(1): 35-41.

12. Pervez, A. & Omkar (2003). Predation potential and handling time estimates of a generalist aphidophagous ladybird, *Propylea dissecta*. *Biological Memoirs*, 29: 91-97.
13. Omkar & Pervez, A. (2003). Influence of prey deprivation on biological attributes of pale morphs of the ladybeetle, *Propylea dissecta* (Mulsant). *Insect Science and Application*, 23(2): 143-148.
14. Dmitriew, C. & Rowe, L. (2007). Effects of early resource limitation and compensatory growth on lifetime fitness in the ladybird beetles (*Harmonia axyridis*). *Journal of Evolutionary Biology*, 20: 1298-1310.
15. Agarwala, B.K., Yasuda, H. & Sato, S. (2008). Life history response of a predatory ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) to food stress. *Applied Entomology and Zoology*, 43 (2): 183-189.
16. Schuder, I., Hommes, M. & Larink, O. (2004). The influence of temperature and food supply on the development of *Adalia bipunctata* (Coleoptera: Coccinellidae). *European Journal of Entomology*, 101: 379-384.
17. Obrycki, J.J., Giles, K.L. & Ormord, A.M. (1998). Interactions between an introduced and indigenous coccinellid species at different prey densities. *Oecologia*, 117: 279-285.
18. Agarwala, B.K., Bardhanroy, P., Yasuda, H. & Takizawa, T. (2001). Prey consumption and oviposition in aphidophagous predator *Menochilus sexmaculatus* (Coleoptera: Coccinellidae) in relation to prey density and adult size. *Environmental Entomology*, 30: 1182-1187.
19. Legaspi, J.C. & Legaspi, B.C. (1998). Life history trade-offs in insects, with emphasis on *Podisus maculiventris* (Heteroptera: Pentatomidae). In: Coll, M. & Ruberson, J.R. (eds): *Predatory Heteroptera: Their ecology and use in biological control*. Entomological Society of America, Thomas Say Publications in Entomology, Laham, pp. 71-87.
20. Stamp, N.E. (2001). Effects of prey quantity and quality on predatory wasp. *Ecological Entomology*, 26: 292-301.
21. Seagraves, M.P. (2009). Lady beetle oviposition behavior in response to the trophic environment. *Biological Control*, 51: 313-322.
22. Maurice, N. & Kumar, A. (2011). Effect of quantity and consumption of food on body weight and development of two species of ladybird beetles. *Annals of Plant Protection Sciences*, 19(1): 59-62.
23. Matsura, T. & Morooka, K. (1983). Influences of prey density on fecundity in a mantis, *Paratenodera angustipennis* (S.). *Oecologia*, 56: 306-312.
24. Zheng, Y., Hagen, K.S., Daane, K.M. & Mittler, T.E. (1993a). Influence of larval dietary supply on the food consumption, food utilization efficiency, growth and development of the lacewing *Chrysoperla carnea*. *Entomologia Experimentalis et Applicata*, 67: 1-7.
25. Zheng, Y., Daane, K.M., Hagen, K.S. & Mittler, T.E. (1993b). Influence of larval food consumption on the fecundity of the lacewing *Chrysoperla carnea*. *Entomologia Experimentalis et Applicata*, 67: 9-14.
26. Yasuda, H. (1995). Effect of prey density on behaviour and development of the predatory mosquito, *Toxorhynchites towadensis*. *Entomologia Experimentalis et Applicata*, 76: 97-103.
27. Omkar, Sahu, J. & Kumar, G. (2010). Effect of prey quantity in a ladybird beetle, *Anegleis cardoni* (Weise) (Coleoptera: Coccinellidae). *International Journal of Tropical Insect Science*, 30(1): 48-56.
28. Dmitriew, C. & Rowe, L. (2011). The effects of larval nutrition on reproductive performance in a food-limited adult environment. *PLoSONE* 6(3): e17399. doi:10.137 1/journal.pone. 0017399.
29. Baumgartner, J., Bieri, M. & Delucchi, V. (1987). Growth and development of immature life stages of *Propylaea 14-punctata* L. and *Coccinella 7-punctata* L. (Col.: Coccinellidae) simulated by the metabolic pool model. *Entomophaga*, 32: 415-423.
30. Hodek, I. & Honek, A. (1996). *Ecology of Coccinellidae*. Kluwer Academic Publishers Dordrecht Boston London, 464 pp.
31. Francis, F., Haubruge, E. & Gaspar, C. (2000). Influence of host plants on specialist/generalist aphids and on the development of *Adalia bipunctata* (Coleoptera: Coccinellidae). *European Journal of Entomology*, 97: 481-485.
32. Lee, J.H. & Kang, T.J. (2004). Functional response of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) to *Aphis gossypii* Glover (Homoptera: Aphididae) in the laboratory. *Biological Control*, 31: 306-310.
33. Hodek, I. & Michaud, J.P. (2008). Why is *Coccinella septempunctata* so successful? (A point-of-view). *European Journal of Entomology*, 105(1): 1.
34. Omkar, Mishra, G., Srivastava, S., Gupta, A.K., & Singh, S.K. (2005a). Reproductive performance of four aphidophagous ladybirds on cowpea aphid, *Aphis craccivora* Koch. *Journal of Applied Entomology*, 129 (4): 217-220.

35 Lucas, E., Demougeot, S., Vincent, C. & Coderre, D. (2004). Predation upon the oblique-banded leafroller, *Choristoneura rosaceana* (Lepidoptera: Tortricidae), by two aphidophagous coccinellids (Coleoptera: Coccinellidae) in the

presence and absence of aphids. *European Journal of Entomology*, 101: 37-41.

36 Dixon, A.F.G. (2000). *Insect Predator-Prey Dynamics, Ladybird Beetles and Biological Control*. Cambridge University Press, Cambridge, 257 pp.

37 Waldbauer, G.P. (1968). The consumption and utilization of food by insect. *Advances in Insect Physiology*, 5: 229-288.

38 Ramdev & Rao, P.J. (1979). Consumption and utilization of castor by semilooper *Achoea janata*. *Indian Journal of Entomology*, 41: 260-266.

39 Smith, B.C. (1965). Effect of food on the longevity, fecundity and development of adult coccinellids. *The Canadian Entomologist*, 97: 760-768.

40 Glen, D.M. (1973). The food requirements of *Blepharidopterus angulatus* (Heteroptera: Miridae) as a predator of the lime aphid, *Eucallipterus tiliae*. *Entomologia Experimentalis et Applicata*, 16: 255-267.

41. Ahlawat, D.S., Singh, H., Singh, D. & Rohilla, H.R. (2008). Predatory potential of ladybird beetle, *Coccinella septempunctata* L. on mustard aphid, *Lipaphis erysimi* (Kalt.). *Journal of Oilseeds Research*, 25 (1): 62-63.

42. Jalali, M.A., Tirry, L. & De Clercq, P. (2009). Food consumption and immature growth of *Adalia bipunctata* (Coleoptera: Coccinellidae) on a natural prey and a factitious food. *European Journal of Entomology*, 106: 193-198.

43. Finlayson, C.J., Alyokhin, A.V., Gross, S. & Porter, E.W. (2010). Differential consumption of four aphid species by four lady beetle species. *Insect Science*, 10 (31): 1-10.

44. Mishra, G., Kumar, B., Shahid, M. & Singh, D. (2011). Evaluation of four co-occurring ladybirds for use as biocontrol agents of the pea aphid, *Acyrthosiphon pisum* (Homoptera: Aphididae). *Biocontrol Science and Technology*, 21: 991-997.

45. Mishra, G., Omkar, Kumar, B. & Pandey, G. (2012). Stage and age specific predation in four aphidophagous ladybird beetles. *Biocontrol Science and Technology*, 22: 463-476.

46. Scriber, J.M. & Slansky, F. (1981). The nutritional ecology of immature insects. *Annual Review of Entomology*, 26: 183-211.

47. Ferran, A. & Larroque, M.M. (1977a). Etude des relations hôte-prédateur: la consommation et l'utilisation d'un puceron, *Myzus persicae* Sulz. par les différents stades larvaires de la Coccinelle *Semiadalia undecimnotata* Schn.en serre. *Agronomie*, 4: 357-376.

48. Ferran, A. & Larroque, M.M. (1977b). Study of host–predator relations: the consumption and utilization of an aphid, *Myzus persicae* Sulz., by the different larval stages of the coccinellid *Semiadalia undecimnotata* Sch. (Coleoptera : Coccinellidae). *Annales de Zoologie, Ecologie Animale*, 9: 665-691.

49. Sharma, D.K., Varma, G.C. & Kishore, L. (1997). Feeding capacity of predators of mustard aphid, *Lipaphis erysimi*. *Journal of Aphidology*, 11: 171-174.

50. Bertram, D. F. & Strathmann, R.R. (1998). Effects of maternal and larval nutrition on growth and form of planktotrophic larvae. *Ecology*, 79: 315-327.

51. Pervez, A. & Omkar. (2004). Prey-dependent life attributes of an aphidophagous aadybird beetle, *Propylea dissecta* (Coleoptera: Coccinellidae). *Biocontrol Science and Technology*, 14(4): 385-396.

52. Boggs, C.L. & Freeman, K.D. (2005). Larval food limitation in butterflies: effects on adult resource allocation and fitness. *Oecologia*, 144: 353-361.

53. Obrycki, J.J. & Orr, C.J. (1990). Suitability of three prey species for Nearctic populations of *Coccinella septempunctata*, *Hippodamia variegata* and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). *Journal of Economic Entomology*, 83: 1292-1297.

54. Giles, K.L., Madden, R.D., Stockland, R., Payton, M.E. & Dillwith, J.W. (2002). Host plants affect predator fitness via the nutritional value of herbivore prey: investigation of a plant-aphid-ladybeetle system. *Biocontrol*, 47: 1-21.

55. Omkar & James, B.E. (2004). Influence of prey species on immature survival, development, predation and reproduction of *Coccinella transversalis* Fabricius (Col., Coccinellidae). *Journal of Applied Entomology*, 28 (2): 150-157.

56. Phoofolo, M.W., Giles, K.L. & Elliott, N.C. (2007). Quantitative evaluation of suitability of the greenbug, *Schizaphis graminum*, and the bird cherry-oat aphid, *Rhopalosiphum padi*, as prey for *Hippodamia convergens* (Coleoptera: Coccinellidae). *Biological Control*, 41: 25-32.

57. Phoofolo, M.W., Elliott, N.C. & Giles, K.L. (2009). Analysis of growth and development in the final instar of three species of predatory Coccinellidae under varying prey availability. *Entomologia Experimentalis et Applicata*, 131: 264-277.