

BioControl **48:** 379–393, 2003. © 2003 *Kluwer Academic Publishers. Printed in the Netherlands.*

Influence of six aphid prey species on development and reproduction of a ladybird beetle, *Coccinella septempunctata*

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Received 18 December 2001; accepted in revised form 27 November 2002

Abstract. Pre-imaginal development, immature survival, and reproduction of a ladybird, Coccinella septempunctata Linnaeus, were studied in response to six aphid species, Aphis craccivora Koch, Aphis gossypii Glover, Aphis nerii Boyer de Fonscolombe, Lipaphis erysimi (Kaltenbach), Myzus persicae (Sulzer) and Uroleucon compositae (Theobald) to quantify their relative suitability as prey. Pre-adult development was shortest (13.93 \pm 0.12 days) when fed on L. erysimi and longest (22.85 \pm 0.10 days) on A. nerii. Immature survival, adult emergence, growth index, relative growth rate, development rate, male and female longevity, oviposition period, fecundity and hatching percent were maximal, i.e. $73.47 \pm 0.89\%$, 90.07 \pm 1.43%, 8.62 \pm 0.23, 1.52 \pm 0.02, 0.07, 81.10 \pm 1.26 days, 85.70 \pm 1.45 days, 69.80 \pm 1.32 days, 1764.10 \pm 8.46, and 87.88 \pm 1.05, respectively when C. septempunctata were fed on *L. erysimi*. The same parameters were minimal, i.e. $43.86 \pm 1.33\%$, $71.65 \pm 2.75\%$, $2.02 \pm 0.08, 0.49 \pm 0.02, 0.04, 44.40 \pm 1.39$ days, 53.50 ± 1.00 days, 16.40 ± 0.60 days, 203.20 ± 11.83 , and 48.68 ± 2.06 , respectively on A. nerii. The weights of different ladybird life stages were maximal after feeding on L. erysimi and minimal on A. nerii. Regression analyses of the data revealed linear relationships between development rate and weight of adult; daily prey consumption and relative growth rate; log weight of adult male and female; and longevity and fecundity of female. On the basis of these findings, the order of suitability of aphid species for C. septempunctata is L. erysimi > M. persicae > A. craccivora > A. gossypii> U. compositae > A. nerii. Thus, the present information can be utilized for the mass rearing of C. septempunctata by supplying the best food and can also help in the prediction of the relative abundance of the ladybird on different aphid infestations in the fields.

Key words: aphid, *Coccinella septempunctata*, Coccinellidae, Coleoptera, fecundity, immature survival, ladybird, pre-adult development, prey species

Introduction

Ladybirds consume a wide variety of prey species including several small phytophagous insects and acarines and are therefore considered as potent predators (Hagen, 1987) and good biocontrol agents. Some ladybirds are predators of aphids, certain others of coccids and there are a few species, which are predaceous on both groups (Agarwala and Ghosh, 1988). *Coccinella septempunctata* Linnaeus is an ubiquitous aphidophagous ladybird, predominant in Indian agroecosystems and of great economic importance (Omkar and Pervez, 2000; Omkar and Srivastava, 2001).

Mere presence of a ladybird at a prey-site was earlier considered as proof of its prey choice. However, this inference was later criticized for its inaccuracy (Hodek and Honek, 1996). All aphid species are not equally suitable and ladybirds exhibit a choice for certain aphid species (Omkar et al., 1997). Prey are categorized into essential, alternative and rejected prey, on the basis of quantitative data on developmental parameters (rate of development, survival and reproductive capacity) (Hodek, 1962; Hodek and Honek, 1996). A few earlier studies have been conducted on the effect of some aphid species on various aspects of *C. septempunctata* (Blackman, 1965, 1967; Kawauchi, 1985; Obrycki and Orr, 1990). In this study, the developmental responses of immature stages and the reproductive responses of adult *C. septempunctata* were investigated in order to quantify the relative suitability of six aphid species as prey, viz. *Aphis craccivora* Koch, *Aphis gossypii* Glover, *Aphis nerii* Boyer de Fonscolombe, *Lipaphis erysimi* (Kaltenbach), *Myzus persicae* (Sulzer) and *Uroleucon compositae* (Theobald).

Materials and methods

Laboratory maintenance

Adult *C. septempunctata* were collected from agricultural fields adjoining the city of Lucknow, India, and brought to the laboratory. Mating pairs were kept in jars (diameter 11.0 cm and height 8.5 cm) covered with fine muslin cloths fastened with rubber bands. They were supplied with a particular species of aphid, viz. *A. craccivora, A. gossypii, A. nerii, L. erysimi, M. persicae* and *U. compositae* on their respective host plant twigs, viz. *Dolichos lablab* Linnaeus (bean), *Lagenaria vulgaris* Seringe (bottle gourd), *Calotropis procera* (Aiton) (milkweed), *Brassica campestris* Linnaeus (mustard), *Solanum tuberosum* Linnaeus (potato) and *Carthamus tinctorius* Linnaeus (safflower), respectively. Dried twigs were replaced with fresh ones after every twenty-four hours. All ladybird stages were maintained at a temperature of 25 ± 2 °C and $65 \pm 5\%$ R.H.

Experimental design

Pre-adult development and immature survival

Effect of prey species was evaluated on the pre-adult development and immature survival of C. septempunctata. For the purpose one hundred eggs were collected from the laboratory maintained stock and kept in a Petri dish (diameter 16.0 cm and height 2.6 cm) until hatching. Moist filter papers were placed at the bottom of the Petri dish to maintain the humidity. The duration between egg laying and eclosion was recorded and the first instars were transferred from Petri dishes to glass beakers (diameter 6.5 cm and height 9.5 cm) using a soft camel hairbrush. A specific aphid species along with host plant twig was supplied during the entire larval life span. To record the consumption by first/second instar, one hundred aphids were provided per glass tube (height 7.5 cm and diameter 5.0 cm). The newly hatched first instars were placed gently, one in each tube in close vicinity to the prey. A fine muslin cloth, secured with a rubber band, covered the open end of the tube. Remaining aphids were counted daily and replaced with fresh ones on host plant twigs every twenty-four hours in order to avoid microbial contamination. A similar method was followed to record the consumption of third and fourth instars, using four hundred aphids per tube. The same procedure was repeated for every aphid species. Early instars of larger aphids, viz., A. craccivora, U. compositae and later instars of smaller aphids viz., A. gossypii, A. nerii, L. erysimi and M. persicae, were selected to standardize the size of prey provided. Gravid females of aphids were not selected because they may reproduce and cause error. The total number of aphids consumed by larvae during larval development was recorded and cast exuviae noted and removed daily to record the number of moults and number of larvae surviving at each stage.

Prepupal and pupal development periods, and the number of pupae formed, were also recorded. The daily prey consumption of adult males and females was recorded by providing two hundred individuals of different aphid species each day, and unconsumed aphids were counted and removed after every 24 h. The longevity of emerged male and female ladybirds on the different prey species was recorded. The experiment was replicated ten times with each aphid species.

Percentage immature survival, adult emergence and development rate (1/developmental period i.e. the period from the day of oviposition to adult emergence) were recorded using the following formulae, and growth index was recorded by the formula proposed by Dubey et al. (1981).

Percent immature survival (%) = $\frac{\text{Number of pupae formed}}{\text{Number of first instars hatched}} \times 100$

Growth index = $\frac{\text{Percent pupation}}{\text{Larval period}}$

Adult emergence (%) = $\frac{\text{Number of adult ladybirds emerged}}{\text{Number of pupae}} \times 100$

Weight of different life stages when fed on different aphid species

Wet weights of different life stages, viz. different instars, prepupae, pupae and adults (male and female) reared on each aphid species (n = 10) were measured separately. Relative growth rate (RGR) was calculated by the following formula.

Relative growth rate (RGR) =

Reproduction on different aphid species

Reproductive responses of the ladybird to feeding on six aphid species in terms of preoviposition period (the period from emergence to first oviposition), oviposition period (the period from first day of oviposition to last day of oviposition) and post oviposition period (period from the last oviposition to the death of the female) were recorded. The lifetime fecundity (total number of eggs laid by each female during her lifetime) was recorded and all the eggs observed to determine egg viability.

Data analysis

The data of the above experiments were subjected to analysis of variance (One way ANOVA) and Bonferroni test for the comparison of means. To determine the relationship between: (1) daily prey consumption and relative growth rate, (2) development rate and the weight of adults, (3) the log weight of male and female, and (4) longevity and fecundity, linear regression analysis was applied following the statistical package, Statistix 4.1 (1994) software.

Results

Pre-adult development and immature survival

The data revealed that when adult ladybirds were fed on six aphid species, the incubation period of eggs varied significantly (F = 141.58; p < 0.001; df = 9; Table 1). The mean durations of first (F = 182.89; p < 0.001; df = 9), second (F = 95.32; p < 0.001; df = 9), third (F = 343.32; p < 0.001; df = 9) and fourth instars (F = 268.96; p < 0.001; df = 9) varied significantly when fed on six aphid species. The prepupal (F = 50.19; p < 0.001; df = 9) and pupal (F = 56.74; p < 0.001; df = 9) periods were also found to vary significantly on the six aphid species. The complete developmental period was shortest (13.93 ± 0.12 days) when fed on *L. erysimi* and longest (22.85 ± 0.10 days) on *A. nerii* (F = 805.55; p < 0.001; df = 9).

Data in Table 2 revealed that the developmental rate of the ladybird varied from 0.07 to 0.04 on six aphid species. The total larval consumption differed significantly (F = 586.30; p < 0.001; df = 9) on all the six aphid species. The daily consumption of male (F = 202.94; p < 0.001; df = 9) and female (F = 128.48; p < 0.001; df = 9) also varied significantly.

Percent immature survival was highest $(73.47 \pm 0.89\%)$ when larvae were fed on *L. erysimi* and lowest $(43.86 \pm 1.33\%)$ on *A. nerii* (F = 29.33; *p* < 0.001; df = 9). The adult emergence was highest $(90.07 \pm 1.43\%)$ after feeding on *L. erysimi* and lowest $(71.65 \pm 2.75\%)$ on *A. nerii* (F = 10.38; *p* < 0.001; df = 9). Growth index of *C. septempunctata* was highest (8.62 ± 0.23) after feeding on *L. erysimi* and lowest (2.02 ± 0.08) on *A. nerii* (F = 154.29; *p* < 0.001; df = 9). The longevity of male (F = 133.41; *p* < 0.001; df = 9) and female ladybirds varied significantly (F = 77.77; *p* < 0.001; df = 9) on six aphid species.

Weight of different life stages

Table 1 revealed that weight of first (F = 260.85; p < 0.001; df = 9) and second instars (F = 297.52; p < 0.001; df = 9) did not vary significantly on the six aphid species. However, on some aphid species the differences in weight were significant as is suggested by the comparison of means. The weight of third (F = 225.84; p < 0.001; df = 9) and fourth instars (F = 1011.31; p < 0.001; df = 9) varied significantly after feeding on six aphid species. The prepupal (F = 581.38; p < 0.001; df = 9) and pupal (F = 864.65; p < 0.001; df = 9) weights also varied significantly when respective larvae were fed on different aphid species. The adult males (F = 1176.12; p < 0.001; df = 9) and females (F = 983.37; p < 0.001; df = 9) showed significant variation in weights when fed on different aphid species. The relative growth rate (RGR) was highest (1.52

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Aphid species		L. erysimi	M. persicae	A. craccivora	A. gossypii	U. compositae	A. nerü	F-value
Incubation period		$2.42\pm0.05^{\rm a}$	$2.84\pm0.03^{ m b}$	$2.98\pm0.04^{ m bc}$	$3.10\pm0.02^{\mathrm{cd}}$	$3.55\pm0.04^{\mathrm{e}}$	$3.64\pm0.04^{\mathrm{ef}}$	141.58
First instar	Duration	$1.72\pm0.03^{\mathrm{a}}$	$1.79\pm0.04^{\mathrm{ab}}$	$1.98\pm0.04^{ m c}$	$2.13 \pm 0.02^{\mathrm{cd}}$	$2.60\pm0.05^{\mathrm{e}}$	$2.96\pm0.02^{ m f}$	182.89
	Weight	$2.26\pm0.03^{\rm a}$	$2.24\pm0.03^{\mathrm{ab}}$	$1.99\pm0.06^{\mathrm{c}}$	$1.31\pm0.03^{ m d}$	$1.20\pm0.03^{ m de}$	$1.07\pm0.01^{ m f}$	260.85
Second instar	Duration	$1.64\pm0.04^{\mathrm{a}}$	$1.84\pm0.07^{ m b}$	$2.18\pm0.03^{\mathrm{c}}$	$2.28\pm0.03^{ m cd}$	$2.55\pm0.05^{\rm e}$	$2.75\pm0.03^{\mathrm{f}}$	95.32
	Weight	5.55 ± 0.06^{a}	$5.33\pm0.03^{\mathrm{ab}}$	$4.54\pm0.07^{\mathrm{c}}$	$4.08\pm0.03^{ m d}$	$3.91\pm0.06^{ m de}$	$3.06\pm0.07^{\mathrm{f}}$	297.52
Third instar	Duration	$1.84\pm0.05^{\rm a}$	$2.00\pm0.05^{ m b}$	$2.34\pm0.04^{ m c}$	$2.49\pm0.02^{\mathrm{cd}}$	$3.11\pm0.03^{\mathrm{e}}$	$3.34\pm0.03^{ m f}$	343.32
	Weight	$10.63\pm0.10^{\mathrm{a}}$	$9.73\pm0.12^{ m b}$	$9.00\pm0.07^{\mathrm{c}}$	$8.60 \pm 0.12^{\mathrm{cd}}$	$8.53\pm0.10^{ m de}$	$6.29\pm0.06^{\mathrm{f}}$	225.84
Fourth instar	Duration	$2.75\pm0.04^{\mathrm{a}}$	2.99 ± 0.03^{b}	$3.24\pm0.09^{ m c}$	$3.50\pm0.03^{ m d}$	$4.49\pm0.08^{\mathrm{e}}$	$5.08\pm0.03^{\mathrm{f}}$	268.96
	Weight	$19.79\pm0.07^{\mathrm{a}}$	$17.91 \pm 0.07^{\mathrm{b}}$	$16.93\pm0.05^{\mathrm{c}}$	$15.95\pm0.11^{\mathrm{d}}$	$13.94\pm0.10^{\mathrm{e}}$	$11.11\pm0.15^{\rm f}$	1011.31
Prepupal period	Duration	$0.74\pm0.02^{\mathrm{a}}$	$0.93\pm0.02^{ m b}$	$0.96\pm0.02^{ m bc}$	$1.03 \pm 0.02^{\mathrm{cd}}$	$1.07\pm0.01^{ m de}$	$1.13 \pm 0.01^{\mathrm{ef}}$	50.19
	Weight	$15.52\pm0.06^{\rm a}$	$14.59\pm0.08^{\mathrm{b}}$	$13.81\pm0.03^{\rm c}$	$12.93\pm0.05^{\mathrm{d}}$	$11.88\pm0.15^{\rm e}$	$8.24\pm0.18^{\rm f}$	581.38
Pupal period	Duration	$2.81\pm0.06^{\rm a}$	$2.92\pm0.06^{\mathrm{ab}}$	$3.16\pm0.05^{ m bc}$	$3.42\pm0.06^{\mathrm{cd}}$	$3.58\pm0.07^{ m de}$	$4.00\pm0.05^{\mathrm{f}}$	56.74
	Weight	$15.05\pm0.03^{\rm a}$	14.13 ± 0.09^{b}	$13.44\pm0.03^{\mathrm{c}}$	$12.29\pm0.05^{ m d}$	$10.77 \pm 0.12^{\mathrm{e}}$	$7.11\pm0.17^{\mathrm{f}}$	864.65
Development	Duration	$13.93\pm0.12^{\rm a}$	$15.24\pm0.08^{\mathrm{b}}$	$16.83 \pm 0.14^{\mathrm{c}}$	$17.94\pm0.13^{\mathrm{d}}$	$20.95\pm0.14^{\rm e}$	$22.85\pm0.10^{\rm f}$	805.55
	Weight							
	Male	$38.20\pm0.26^{\rm a}$	$33.94\pm0.13^{\mathrm{b}}$	$29.88\pm0.22^{\rm c}$	$27.09\pm0.15^{\mathrm{d}}$	$23.78\pm0.07^{\mathrm{e}}$	$20.78\pm0.23^{\mathrm{f}}$	1176.12
	Female	40.63 ± 0.22^{a}	$37.69\pm0.18^{\mathrm{b}}$	$33.41 \pm 0.11^{\circ}$	$31.25\pm0.18^{\mathrm{d}}$	$25.94 \pm 0.14^{\mathrm{e}}$	$22.34\pm0.38^{\mathrm{f}}$	983.37
Values are Mean ± Duration is in days. Weight is in mg. Means followed by	S.E. the same le	tters in the same 1	tow are not signifi	icantly different at	<i>p</i> < 0.001.			

Table 1. Duration and weight of different life stages of C. septempunctata on different aphid species (n = 10)

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Table 2. Growth and repu	roduction of C. sep	<i>tempunctata</i> on diff	ferent aphid species	(n = 10)			
Aphid species	L. erysimi	M. persicae	A. craccivora	A. gossypii	U. compositae	A. nerü	F-value
% immature survival	73.47 ± 0.89^{a}	$66.60 \pm 0.81^{\mathrm{ab}}$	$64.24 \pm 2.22^{\rm bc}$	$61.15 \pm 3.08^{\mathrm{cd}}$	52.13 ± 2.39^{e}	$43.86\pm1.33^{\rm f}$	29.33
Growth index	8.62 ± 0.23^{a}	$7.38\pm0.14^{ m b}$	$5.13\pm0.22^{ m c}$	$4.98 \pm 0.25^{\circ}$	$3.54\pm0.20^{ m d}$	$2.02\pm0.08^{\mathrm{e}}$	154.29
Adult emergence (%)	90.07 ± 1.43^{a}	$88.50\pm1.17^{\mathrm{ab}}$	$85.03 \pm 1.51^{\mathrm{ab}}$	81.14 ± 2.11^{ab}	$80.17 \pm 2.93^{\rm bc}$	$71.65\pm2.75^{\mathrm{d}}$	10.38
Larval consumption	765.70 ± 6.81	701.70 ± 1.81	661.60 ± 3.85	603.90 ± 5.12	542.50 ± 4.55	457.30 ± 4.03	586.30
Daily consumption of male	64.00 ± 1.29^{a}	59.01 ± 1.09^{ab}	$49.04 \pm 1.30^{\circ}$	43.60 ± 1.74^{cd}	25.20 ± 0.89^{e}	$19.38 \pm 1.52^{\mathrm{f}}$	202.94
Daily consumption of female	72.14 ± 1.43^{a}	65.32 ± 1.45^{b}	59.16 ± 1.28^{c}	53.81 ± 1.55^{cd}	34.75 ± 1.52^{e}	$26.34 \pm 2.11^{\mathrm{f}}$	128.48
Male longevity (days)	81.10 ± 1.26	74.00 ± 0.89	68.20 ± 1.43	59.20 ± 1.47	50.10 ± 0.71	44.40 ± 1.39	133.41
Female longevity (days)	85.70 ± 1.45	80.00 ± 0.95	76.60 ± 1.40	73.70 ± 1.84	62.50 ± 1.25	53.50 ± 1.00	TT.TT
Development rate (day ⁻¹)	0.07	0.07	0.06	0.06	0.05	0.04	
Relative growth rate (RGR)	1.52 ± 0.02	1.27 ± 0.03	0.99 ± 0.01	0.86 ± 0.02	0.57 ± 0.01	0.49 ± 0.02	440.69
Preoviposition period (days)	8.20 ± 0.52^{a}	12.30 ± 0.63^{b}	$14.90 \pm 0.55^{\circ}$	$16.40\pm0.58^{\mathrm{cd}}$	$18.20 \pm 0.55^{\mathrm{de}}$	20.40 ± 0.58^{e}	56.62
Oviposition period (days)	69.80 ± 1.32^{a}	$57.90\pm0.98^{\mathrm{b}}$	50.70 ± 1.07^{c}	44.80 ± 1.55^{d}	30.20 ± 1.07^{e}	$16.40\pm0.60^{\mathrm{f}}$	286.31
Post oviposition period (days)	7.50 ± 0.37^{a}	10.00 ± 0.42^{b}	$10.90 \pm 0.46^{\rm bc}$	12.60 ± 0.40^{cd}	14.10 ± 0.57^{d}	$16.70 \pm 0.93^{\mathrm{e}}$	33.47
Fecundity	1764.10 ± 8.46^{a}	$1198.50 \pm 0.08^{\rm b}$	$1060.70\pm 25.83^{\rm c}$	739.20 ± 31.99^{d}	$488.10 \pm 16.41^{\rm c}$	$203.20 \pm 11.83^{\rm d}$	345.70
% Hatchability	87.88 ± 1.05^{a}	$79.92\pm0.63^{ m b}$	74.74 ± 0.73^{c}	71.12 ± 0.90^{d}	$58.57 \pm 1.27^{\mathrm{e}}$	$48.68\pm2.06^{\rm f}$	106.38
Values are Mean \pm S.E. Means followed by the sa	ame letters in the se	ame row are signific	antly different at p	< 0.001.			

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 \pm 0.02) after feeding on *L. erysimi* and lowest (0.49 \pm 0.02) on *A. nerii* (F = 440.69; *p* < 0.001; df = 9) (Table 2). A linear and positive correlation (Y = 14.56 + 40.84X; r² = 0.8484; *p* < 0.001) was found to exist between RGR and daily prey consumption (Figure 1).

Figure 2 shows the presence of a linear relationship between developmental rate and weight of adult ladybirds (Y = -1.908 + 579.17X; r² = 0.9577; p < 0.001) and Figure 3 shows a positive correlation between the log weight of male and female ladybirds fed on different aphid species (log Y = 0.0547 + 0.9912 log X; r² = 0.9668; p < 0.001).

Reproduction on different aphid species

Table 2 revealed that the non-reproductive, i.e. pre-oviposition (F = 56.62; p < 0.001; df = 9) and post-oviposition periods (F = 33.47; p < 0.001; df = 9) and reproductive period, i.e. oviposition period (F = 286.31; p < 0.001; df = 9), varied significantly when the ladybirds were fed on different aphid species. Fecundity varied significantly (F = 345.70; p < 0.001; df = 9) between aphid species and regression analysis revealed a positive correlation between longevity and fecundity (Figure 4) with regression equation Y = 53.941 + 0.0199X (r² = 0.7785; p < 0.001). The percentage hatchability of eggs also varied significantly (F = 106.38; p < 0.001; df = 9) when ladybirds were fed on different aphid species.

Discussion

Pre-adult development and immature survival

The increased growth, development and survival rates of *C. septempunctata* when fed *L. erysimi* may be attributed to (1) the presence of higher protein levels in this species (Atwal and Sethi, 1963), and/or (2) their higher consumption, which could be due to higher palatability. Incubation period of eggs was lowest on *L. erysimi* and highest on *A. nerii*. This perhaps indicates the role of adult diet in the rate of development of embryos. The finding is in close agreement with that recorded for *Cheilomenes sexmaculata* (Fabricius) (Chaudhary et al., 1983) and *Brumoides suturalis* (Fabricius) (Gautam, 1990). The aphid species in decreasing order of development rate of ladybird was *L. erysimi* > *M. persicae* > *A. craccivora* > *A. gossypii* > *U. compositae* > *A. nerii* with a similar order for the amount of food consumed by the larvae. Aphid species that were consumed in lesser amounts resulted in a longer larval development period of *C. septempunctata*. The developmental rate of ladybird instars was thus found to be proportionate to the amount of food



Figure 1. Relationship between relative growth rate (RGR) and per day prey consumption by female C. septempunctata on different species of aphids. Figure 2. Relationship between adult weight of female (mg) in relation to development rate of C. septempunctata aphids.

Figure 3. Relationship between the logarithm of the weight of males and female of C. septempunctata on different species of aphids. Figure 4. Relationship between longevity and fecundity of C. septempunctata on different species of aphids.

eaten by them. Reduced consumption probably leads to reduced nutritional levels, thus having a substantial effect on larval development. Blackman (1967) also noticed the difference in larval development of *C. septempunctata* after being fed on different aphids (viz. *M. persicae, Aphis fabae* Theobald, *Acyrthosiphon pisum* (Harris), *Megoura viciae* Buckton, *Brevicoryne brassicae* (Linnaeus) and *Aphis sambuci* (Linnaeus)). The reduced consumption of some aphids has been ascribed to the presence of certain alkaloids or unsuitable chemicals, not suitable to the constitution and metabolism of the ladybird (Hodek, 1956; Okamoto, 1966). The toxicity of certain aphid species needs to be confirmed by chemical analysis of body contents.

The lower consumption of those aphids that were less suitable for growth and development of ladybirds might be due to (1) sensory perception prior to consumption, and/or (2) to a prior bad learning experience. Reduced consumption, in possible response to the chemical constituents, might maintain the unwanted chemicals below harmful levels but still ensure survival. A reduction in immature survival on those aphids that were consumed in lesser amounts was also observed. Our finding is in agreement with results reported by Dixon (2000). Possible reasons for increased mortality of immature stages on the lesser-consumed aphids include (1) slow starvation resulting from lower consumption and/or (2) inability of the ladybird's metabolism to detoxify or sequestrate the alkaloids and other unsuitable chemicals. This has also been suggested by Olszak (1986, 1988). Both, the higher levels of proteins (Atwal and Sethi, 1963) and absence of unsuitable chemicals might be the cause of higher consumption and improved immature survival on *L. erysimi*.

In the present study, the response of C. septempunctata to A. craccivora and A. nerii was contradictory to earlier findings. A. craccivora was recorded as being lethal for many ladybird species viz., C. septempunctata (Azam and Ali, 1970), Harmonia axvridis (Pallas) (Hukusima and Kamei, 1970) and Semiadalia undecimnotata (Schneider) (Hodek, 1960). A. craccivora from the host plant Robinia pseudoacacia Linnaeus was found to be toxic due to the presence of amines, canavanine and ethanolamine, sequestered from the host plant (Obatake and Suzuki, 1985). Contrary to these studies, Hodek (1960) reported A. craccivora (on Vicia faba Linnaeus) as an essential food for C. septempunctata. A. nerii, living on the host plant Nerium oleander Linnaeus, was also reported to be toxic to the ladybirds, C. septempunctata, S. undecimnotata, Propylea quatuordecimpunctata (Linnaeus), Adalia bipunctata (Linnaeus), Harmonia dimidiata (Fabricius), C. septempunctata brucki Linnaeus and Coccinella repanda Thunberg (Iperti, 1966; Tao and Chiu, 1971). A high amount of cardiac glycosides cardenolides, particularly oleanderin and neriin were found to be responsible for the toxicity of oleander (Rothschild et al., 1970). Twenty-five cardenolides were identified in *N. oleander*, 17 of which were found in aphids feeding on it and 20 in their honeydew (Malcolm, 1990). These studies confirm the effect that a host plant can have on the palatability and suitability of the aphid species to ladybirds. Differential distribution of cardenolides in the plant also affected the palatability of aphids, as floral-feeding *A. nerii* were found to be more palatable than leaf feeding *A. nerii* to adults of *Hippodamia convergens* Guerin (Bristow, 1991). The different seasons of the year also influence palatability and suitability of the prey (Takeda et al., 1964).

Differential consumption of the aphid species affected the longevity of adults. This observation is in conformity with those of Milevoj (1997) and Lakhanpal and Raj (1998). The growth rate of larvae of *C. septempunctata* was found to be proportionate to the amount of food eaten. The relative growth rate (RGR) refers to the conversion of aphid to ladybird biomass. RGR and development rate of ladybirds were highest on the most suitable prey and lowest on the least suitable prey. This indicates that the species shows tendency of a specific predator, as also reported by Thompson (1951) and Obrycki and Orr (1990).

Weight of different life stages

The highest wet weights of different ladybird stages were attained after feeding on L. erysimi, and this may be ascribed to its suitable nutritive content (Atwal and Sethi, 1963), and high consumption rate by ladybirds. All the aphid species offered were consumed by the larvae, but they were not equally suitable, as the developmental period and adult weight of ladybirds, reared on these aphids varied greatly. The first, second and third instars showed relatively less difference in weight when fed on different aphid species, but fourth instars, pupae and adults had significantly different weights. It is possible that early instars might be consuming any available aphid, without discrimination, to survive to the next instar and attain a certain critical weight. Later instars and adults might perhaps be more discriminating towards the prey and thus, consume their preferred prey in large amounts while consuming less of the non-preferred one. This can possibly be attributed to the achievement of a threshold level of development and nutrition required to reach the adult stage in the earlier instars. However, the larval development of C. septempunctata was not completed when they were fed on A. sambuci, an inadequate food (Hodek, 1956, 1957a, b).

The increased food intake of suitable prey results in increased weight and development of *C. septempunctata*. The faster developing larvae consumed more prey and developed into larger adults. Thus, the size of the ladybirds is a consequence of the relative effect of food quantity as well as quality.

The rate of development is directly related to weight. The linear relationship between per day prey consumption and relative growth rate confirmed that the growth rate (mg/day) of instars increased linearly with the increasing rate of food consumption, as also recorded in *A. bipunctata* (Baumgaertner et al., 1981) and *H. convergens* (Rodriguez and Miller, 1995).

Reproduction on different aphid species

The shortest preoviposition period of *C. septempunctata* was after feeding on *L. erysimi*, and this suggests that the increased quantity of high quality food decreased the length of the preoviposition period. This is also supported by the findings of Rhamhalinghan (1985). The decreased consumption of less suitable foods and/or the presence of alkaloids probably affect the pre-adult development, resulting in slower sexual maturation and a longer preoviposition period on unsuitable aphids. This view is supported by the findings for *H. axyridis* (Hukusima and Kamei, 1970) and *Propylea japonica* Thunberg (Kawauchi, 1981).

High consumption of suitable food (along with the suitable nutrients) supports early ovariole maturation and provides energy to sustain a longer oviposition period, while the reduced consumption of less suitable food affects, and probably slows down, ovariole development. This lends support to the hypothesis that a certain amount of food is necessary for maturation of ovarioles in *C. septempunctata* (Honek, 1980). A similar finding, that quality and quantity of food affects the oviposition period, was also recorded for *M. sexmaculatus* (Agarwala and Choudhuri, 1995). Thus, when the ladybirds were fed on suitable aphids, the pre-reproductive period was shortened, while the consumption of less suitable food increased the non-reproductive phase.

The effect of quality, as well as quantity, of food was also seen on fecundity and longevity. There was a linear relationship between the food consumed and longevity and fecundity of the ladybird. Linear relationship between longevity and fecundity suggests that longevity may be an important determinant of fecundity. These findings are in conformity with those recorded for *C. septempunctata* (Rhamhalinghan, 1987; Kawauchi, 1991).

Conclusion

The data on development rate, immature survival, adult emergence, larval and adult prey consumption, longevity of male and female, weight of different life stages, relative growth rate and reproduction on different prey species suggest that: (i) *C. septempunctata* feeds on all six prey species offered,

(ii) quantitative data on oviposition period, fecundity and hatching percent on different prey species was in the following decreasing order: L. erysimi > M. persicae > A. craccivora > A. gossypii > U. compositae > A. nerii which indicates the comparative suitability of prey. (iii) L. erysimi was the most suitable amongst the tested aphid species for the ladybird, C. septempunctata, (iv) comparatively lower development and reproduction rates of the ladybird on M. persicae, A. craccivora and A. gossypii (compared to L. erysimi) suggests that they are effective for the growth, development and reproduction of C. septempunctata in the absence of the most suitable prey, (v) the response of the ladybird towards U. compositae and A. nerii shows that they enable survival of C. septempunctata (when more suitable prey are scarce) by providing energy but not the required nutrients in the required amount. Thus, the present information can be utilized for the mass rearing of C. septempunctata by supplying the best food, and can also help in the prediction of the relative abundance of the ladybird on different aphid infestations in the field.

Acknowledgements

Authors are thankful to Dr. D.J. Ponsonby, Canterbury Christ Church College, Science Department Research Group, Canterbury, UK for critically reviewing the manuscript, and Indian Council of Agricultural Research, New Delhi, India for financial assistance.

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