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Monotypic prey-mediated development, survival and life table attributes of a ladybird beetle *Anegleis cardoni* (Coleoptera: Coccinellidae) on different aphid species

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Abstract. Successful mass production of biocontrol agents is a prerequisite to their effective use in the field. Thus in the present study the suitability of ten aphid species of a ladybird beetle *Anegleis cardoni* (Weise) in terms of growth, development, survival and mortality life table attributes was assessed for the purpose of mass production. The study revealed that the developmental duration of the immature stages of *A. cardoni* was shortest when fed on *Uroleucon compositae* (Theobald), *Rhopalosiphum maidis* (Fitch), *Hyadaphis coriandri* (Das) and *Myzus persicae* (Sulzer) in comparison with other aphid species. Immature survival, development rate, adult weight and growth index were also highest when *A. cardoni* larvae were fed on these aphids, while lowest when fed on *Hysteroneura setariae* (Thomas) and *Ceratovacuna silvestri* (Takahashi). Any larva of *A. cardoni* did not reach adult stage when fed on *Aphis nerii* Boyer de Fonscolombe; therefore it may be considered as a toxic prey. Life table data revealed that the overall mortality prior to adult stage was lowest in *U. compositae* and highest in *C. silvestri.* The first instars suffered the highest mortality in comparison with other instars on all the aphid species tested. However, the life expectancy for each aphid species as prey revealed a continuous decline with the advancement of age. Thus among all the ten aphid species tested, *U. compositae*, *R. maidis*, *H. coriandri* and *M. persicae* were found equally suitable for mass production of *A. cardoni*.

Key words: *Anegleis cardoni*, aphid prey, development, life expectancy, mortality life table, survival

Introduction

Insect predators have been grouped as generalists and specialists, with both having variable uses in the biological control of insect pests. Owing to their wide prey range, generalist predators are sometimes considered as less useful in pest management (Harwood *et al.*, 2004; Harper *et al.*, 2005), as they consume both alternative as well as the target prey. However, they may be quite useful in the management of pest complexes of crops. Specialists, on the other hand, consume a single, or closely related species. Despite their differential suitability for biological control, it is essential to determine the prey against which the predator is likely to be more effective. For this purpose, the assessment of prey suitability in terms of development and survival is important.

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Ladybirds are one of the important predatory biological control agents. Most predatory ladybirds feed on either aphids or coccids (a few feed on both), while some feed on mites, adelgids, aleyrodids, chrysomelid larvae and psyllids as well (Dixon, 2000). In the absence of natural prey some of these predaceous ladybirds are known to feed on fungal spores, pollen, honeydew and nectar (Lundgren, 2009). Aphidophagous ladybirds are usually generalists with their prey range categorized into essential, alternative and rejected food (Hodek and Honek, 1996). Predatory ladybirds rely on essential prey to support their reproduction and on alternative prey for survival (Hodek, 1962; Mills, 1981). Malcolm (1992) coined the terms included, peripheral and excluded as alternatives to essential, alternative and rejected prey. Rejected prey is avoided every time, even in the face of the consequences of starvation, to death. Michaud (2005) differentiated prey suitability as optimal, adequate and marginal.

This difference in prey suitability has been attributed to their nutritive value (Phoofolo *et al.*, 2007), costs associated with their capture (Rana *et al.*, 2002) and also their assimilation and utilization of nutrients and energy post prey consumption (Bilde and Toft, 1999; Vivan *et al.*, 2003). Predators may be satiated either by quantitatively or qualitatively selecting the prey for consumption. A quantitatively high but qualitatively poor prey consumes much energy of the predator, while a quantitatively low, but qualitatively high, food is likely to be beneficial for the predator allowing much gain in nutrition and energy. High-quality prey provide better growth and development with lower mortality, although larvae sometimes do not show a preference for high-quality prey (Ferrer *et al.*, 2008). Larvae and adults may differ in nutritional requirements, i.e. a prey suitable for larval development may not be suitable for adult reproduction (Michaud, 2000, 2005). Although aphid prey suitability has been studied for many ladybird beetles, *viz. Adalia bipunctata* L. (Kalushkov, 1998), *Coccinella septempunctata* L. (Omkar and Srivastava, 2003), *Coccinella transversalis* (Fab.) (Babu, 1999; Omkar and James, 2004), *Propylea dissecta* (Mulsant) (Pervez and Omkar, 2004; Omkar and Mishra, 2005), *Micraspis discolor* (Fab.) (Omkar, 2006) (all Coleoptera: Coccinellidae) and many more, it is poorly or almost not studied in the ladybird beetle *Anegleis cardoni* (Weise) (Coleoptera: Coccinellidae).

Anegleis cardoni is a medium-sized ladybird beetle. It is bright yellow with one black median stripe at the joint of both the elytra and two linear markings (one is inwardly and other one is outwardly curved) on each elytron. It occurs in southern and northern parts of India (Puttarudriah and Channabasavanna, 1953; Ghorpade, 1979). Omkar and Bind (1993) reported *A. cardoni* from Lucknow. It is reported to feed voraciously on whiteflies (Ramani *et al.*, 2002) and scale insect pests (Sundararaj, 2008). Afroze (2000) studied the feeding of *A. cardoni* on aphids (*viz. Aphis gossypii* Glover, *Brevicoryne brassicae* (L.), *Macrosiphum miscanthi* Takahashi, and *M. pisi* Kltb. [all Hemiptera: Aphididae]) and coccids and pseudococcids. Besides this, it is also a predator of *Aphis craccivora* Koch, *A. gossypii* and *Lipaphis erysimi* (Kalt.) (all Hemiptera: Aphididae) (Omkar *et al.*, 2009) and many other aphid species (Aphids of Karnataka; http://www.aphidweb.com). Therefore, this study was designed to assess prey suitability for *A. cardoni* in terms of growth, development and survival on ten locally abundant aphid species to answer the following two questions: (a) do the different aphid species provide an equal chance for growth and development of *A. cardoni*?, and (b) which aphid species ensures faster development and higher survival when *A. cardoni* is fed on a monotypic diet? Results will help in identifying the aphid(s) that are more suitable for the enhanced production of *A. cardoni* and also in determining the target prey against which *A. cardoni* can be used as a biological control agent in the field.

Materials and methods

Laboratory maintenance

Ten locally available, aphid–host plant complexes, *viz. Uroleucon compositae* (Theobald) (Hemiptera: Aphididae) from safflower [*Carthamus tinctorius* Linnaeus (Asteraceae)]; *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae) from pea [*Pisum sativum* Linnaeus (Leguminosae)]; *Rhopalosiphum maidis* (Fitch) (Hemiptera: Aphididae) from sorghum [*Sorghum bicolor* (Linnaeus) Moench (Poaceae)]; *Rhopalosiphum padi* (Linnaeus) (Hemiptera: Aphididae) from wheat [*Triticum aestivum* Linnaeus (Poaceae)]; *Myzus persicae* Sulzer (Hemiptera: Aphididae) from black nightshade [*Solanum nigrum* Linnaeus (Solanaceae)]; *Hysteroneura setariae* (Thomas) (Hemiptera: Aphididae) from Bermuda grass [*Cynodon dactylon* (L) Pers. (Poaceae)]; *B. brassicae* (Linnaeus) from cabbage [*Brassica oleracea* Linnaeus (Brassicaceae)]; *Hyadaphis coriandri* (Das) (Hemiptera: Aphididae) from coriander [*Coriandrum sativum* Linnaeus (Apiaceae)]; *Aphis nerii* Boyer de Fonsclombe (Hemiptera: Aphididae) from milkweed [*Calotropis procera* (Aiton) (Asclepiadaceae)] and *Ceratovacuna silvestri* (Takahashi) (Homoptera: Aphididae) from bamboo [*Bambusa arundinacea* (Retzius) Willd. (Poaceae)] were chosen for the study.

To establish a stock culture, adults of *A. cardoni* were collected from False Ashoka (*Polyalthia longifolia* Sonn. [Annonaceae]) trees located on the University of Lucknow campus, India (26°50′N, 80°54′E). Adults were paired and allowed to mate in Petri dishes (9.0 × 1.5 cm) in an environmental test chamber (ETC) at 27 ± 2°C, 65 ± 5% relative humidity and a 14 h light–10 h dark photoperiod, and supplied with *ad libitum* monotypic aphid diet (one of the above) together with host plant leaves, collected from the field. After egg laying, the adults were shifted to a fresh Petri dish (size as above). Post hatching, the larvae were reared in glass beakers (9.5 × 6.5 cm) until adult emergence on the same aphid species, as provided to the parental generation. The aphid supply was replenished every 24 h. F_1 adults were further mated and eggs laid by the females were used for the experimental study. Monotypic supply of the above listed aphid–host plant complexes was maintained throughout the study.

Experimental design

Immature development and survival

To evaluate the larval performance of the different aphid species, 100 eggs were randomly selected from the stock culture and kept in ETC under controlled abiotic conditions. The incubation period and the number of eggs that were hatched were recorded. The hatched larvae were transferred to glass beakers (size as above). Each beaker consisted of five larvae, which were provided with a sufficient amount of aphids together with host plant leaves. Care was taken to provide the same aphid–host plant complex to the larvae, as was provided to their parental stock. Aphid supply together with host plant leaves was replenished every 24 h. Mean values per beaker were considered as values of a replicate and were used for analysis. The number of larvae surviving to the next stage was recorded until adult emergence. The developmental durations of each instar, pre-pupa and pupa were also recorded. All observations were taken twice a day at 12-hourly intervals. The fresh weight of the adults was recorded within 24 h after emergence.

The percentage of immature survival (number of adults emerged/number of first instars × 100), percentage of pupation (number of pupae/number of first instars × 100), developmental rate (1/total developmental period), growth index (percentage of pupation/mean larval duration), generation survival (number of females that emerged/number of first instars) and sex ratio (number of females/total adult emergence) were recorded. The experiment was conducted on each of the ten aphid species.

Data analysis

The results were subjected to one-way ANOVA and the means were compared using Tukey's highly significant differences (HSD) test with $\alpha = 0.05$ (MINITAB, 2003). To investigate the relationship of the rate of development with the sex ratio and weight of adults, Pearson's correlation coefficient was used to test for a correlation between sex ratio and development rate, development rate and weight of the female, and log weight male and log weight female.

Life table parameters

Life table analysis is an important tool in ecology to assess the performance of a predator. Life table attributes were calculated following Morris and Miller (1954) and Southwood (1978):

(a) Age-specific life table

For the construction of an age-specific life table, the total number of larvae that survived and died were recorded daily and the following parameters were calculated:

x = age in days
l_x = age-specific survival, i.e. the number of individuals that survived to enter the xth age interval
d_x = the number dying within xth age interval
$100q_x$ = apparent mortality, d_x as a percentage of l_x

Life expectancy. This is the average life expected or average life remaining for the individuals of *A. cardoni* of a particular stage (x) and was calculated as:

$$[e_x = T_x/L_x]$$

where L_x = the average number alive during any particular stage, calculated as:

$[L_x = l_x + (l_x + 1)/2]$ (where l_x = the total number surviving at the beginning stage)

T_x = the total number of individuals of stage units beyond the stage x, calculated as:

$[T_x = L_x + (L_x + 1) + (L_x + 2) \cdots + L_w]$ (where L_w is the last stage interval).

(b) Stage-specific life table

Stage-specific survival and mortality of eggs, larvae and pupae were recorded for the construction of stage-specific life tables.

x = stage (i.e. eggs, larvae, pupae and adults)

l_x = stage-specific survival, i.e. number of individuals surviving at the beginning of stage x
d_x = number dying within the age interval x
$100q_x$ = apparent mortality, d_x as a percentage of l_x
$100r_x$ = real mortality, d_x as a percentage of the original cohort size
k = a dimensionless measure of mortality within the age interval of x
K = total of k values, i.e. κ
S_x = survival rate of a stage.

Mortality:survivor ratio (MSR). This shows the increase in the population that would have occurred if the mortality in the particular stage (x) had not occurred. This was calculated for a particular stage as:

$$\text{MSR} = [\text{mortality in the particular stage}/ l_x \text{ of subsequent stage}]$$

Indispensable mortality (IM). The mortality that would not occur in a population, if the factor causing it is not allowed to operate and was calculated as:

$$\text{IM} = [\text{total number of adults emerged}] \times [\text{MSR of the particular stage}].$$

Results

Immature development and survival

When the larvae of *A. cardoni* were fed on *A. nerii*, predator larvae did not develop to the adult stage. The larvae died in the third instar stage. The developmental durations of the first and second instars on *A. nerii* were 4.37 ± 0.14 and 4.99 ± 0.08 days, respectively.

Results revealed an insignificant effect of prey species on incubation period ($P = 0.978$, $F = 0.26$, df = 8, 89) and pre-pupal period ($P = 0.878$, $F = 0.46$, df = 8, 89). The incubation periods were found to be minimum and equal (4.00 ± 0.21, 4.00 ± 0.15, 4.00 ± 0.15 and 4.00 ± 0.21 days) for *U. compositae*, *R. maidis*, *M. persicae* and *H. coriandri*, respectively. However, it was found to be maximum (4.20 ± 0.13 days) on *C. silvestri.* The pre-pupal period was found to be shortest (1.84 ± 0.10 days) when the larvae were fed on *U. compositae* and longest (2.13 ± 0.20 days) when fed on *C. silvestri* (Fig. 1).

Significant effects of prey species were recorded on the durations of the first ($P = 0.001$, $F = 14.09$, df = 8, 89), second ($P = 0.001$, $F = 16.01$, df = 8, 89), third ($P = 0.001$, $F = 8.39$, df = 8, 89), and fourth instars ($P = 0.001$, $F = 11.24$, df = 8, 89) and the pupal period ($P = 0.001$, $F = 14.01$, df = 8, 89). The developmental duration of the first instar was

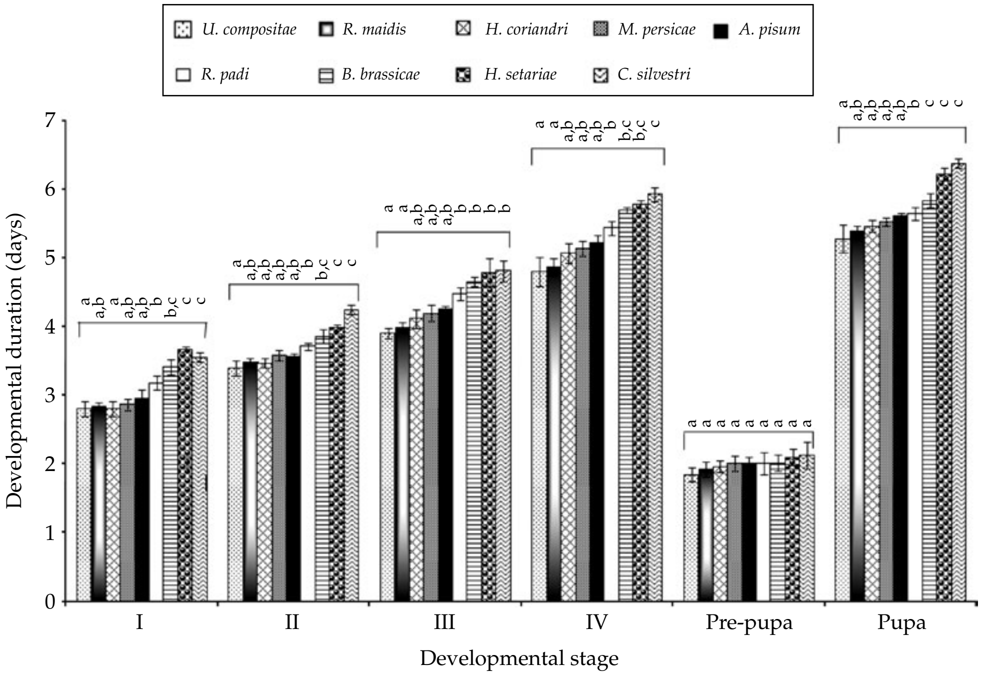

Fig. 1. Developmental durations (days) of different immature stages of *Anegleis cardoni*, fed on different aphid species. Different letters in a stage mean significant differences at the 5% level (Tukey's test); same letters mean non-significant differences at the 5% level.

Table 1. Developmental parameters of *Anegleis cardoni* when fed on different aphid species (df = 8, 89)

Aphid species	Developmental parameters							
	Immature survival (%)	Pupation (%)	Female wt (mg)	Male wt (mg)	Development rate	Growth index	Generation survival	Sex ratio
U. compositae	90.00 ± 4.47b	90.00 ± 4.47a	7.39 ± 0.24c	6.96 ± 0.25c	0.039 ± 0.00d	6.05 ± 0.30b	0.44 ± 0.06a	0.47 ± 0.05
R. maidis	88.00 ± 4.42b	90.00 ± 4.47a	7.11 ± 0.20bc	6.64 ± 0.23c	0.038 ± 0.00cd	5.92 ± 0.29b	0.50 ± 0.04a	0.57 ± 0.05
H. coriandri	88.00 ± 6.11b	90.00 ± 4.47a	6.90 ± 0.15bc	6.21 ± 0.17bc	0.037 ± 0.00cd	5.83 ± 0.29b	0.48 ± 0.07a	0.56 ± 0.07
M. persicae	90.00 ± 4.47b	92.00 ± 4.42a	6.86 ± 0.24bc	5.81 ± 0.29b	0.037 ± 0.00c	5.84 ± 0.28b	0.46 ± 0.06a	0.50 ± 0.06
A. pisum	86.00 ± 4.27b	88.00 ± 4.42a	6.40 ± 0.22b	5.86 ± 0.24b	0.036 ± 0.00c	5.51 ± 0.28b	0.42 ± 0.04a	0.48 ± 0.03
R. padi	86.00 ± 5.21b	88.00 ± 4.42a	6.22 ± 0.28ab	5.50 ± 0.25ab	0.035 ± 0.00bc	5.24 ± 0.26b	0.42 ± 0.04a	0.49 ± 0.03
B. brassicae	82.00 ± 5.54ab	86.00 ± 5.21a	5.93 ± 0.21ab	5.22 ± 0.15ab	0.034 ± 0.00b	4.89 ± 0.30ab	0.42 ± 0.04a	0.52 ± 0.04
H. setariae	74.00 ± 5.21ab	80.00 ± 4.22a	5.81 ± 0.12ab	5.14 ± 0.16ab	0.033 ± 0.00ab	4.40 ± 0.23ab	0.36 ± 0.03a	0.49 ± 0.03
C. silvestri	64.00 ± 5.81a	74.00 ± 6.00a	5.56 ± 0.17a	4.90 ± 0.14a	0.032 ± 0.00a	4.00 ± 0.32a	0.32 ± 0.05a	0.50 ± 0.09
F-values	2.87*	1.47 NS	9.25**	10.55**	25.63**	6.43**	1.36 NS	0.41 NS

Values are means (±SE). Different letters per column indicate values to be statistically different.
* and ** indicate *F*-values to be significant at $P < 0.01$ and $P < 0.001$, respectively; Tukey's test range = 4.51; df = 8, 89.
NS indicates *F*-values to be non significant at $P > 0.05$.

shortest (2.80 ± 0.11 days) on *U. compositae* and longest (3.67 ± 0.03 days) on *H. setariae.* The developmental durations of the second, third and fourth instars and pupa were the shortest (3.39 ± 0.11, 3.90 ± 0.08, 4.79 ± 0.21 and 5.27 ± 0.20 days, respectively) when fed on *U. compositae* and longest (4.24 ± 0.06, 4.81 ± 0.15, 5.92 ± 0.11 and 6.37 ± 0.07 days, respectively) when fed on *C. silvestri.* The total development period was also found to be shortest (26.00 ± 0.47 days) when fed on *U. compositae* and longest (31.21 ± 0.42 days) when fed on *C. silvestri.*

The mean weights of the males and the females, the percentage of immature survival, the development rate and growth index varied significantly, being highest when fed on *U. compositae*, *R. maidis*, *H. coriandri* and *M. persicae*, while being lowest when fed on *C. silvestri* and *H. setariae* (Table 1). The percentage of pupation, generation survival and sex ratio were not found to significantly differ with the aphid species consumed.

Correlation analysis revealed a positive correlation between development rate and weight of female ($r = 0.547$, $P = 0.001$) and log weight male and log weight female ($r = 0.736$, $P = 0.001$). Development rate, however, showed insignificant correlation with sex ratio ($r = 0.127$, $P = 0.223$).

Life table parameters

(a) Age-specific life table

Data revealed that age-specific survival was highest in *R. maidis* and lowest in *C. silvestri* (Fig. 2). Apparent mortality was lowest when the larvae of *A. cardoni* were fed on *R. maidis* and highest when they were fed on *C. silvestri.* Results revealed that as the larvae passed on to the next age interval (x), their life expectancy subsequently decreased (Fig. 3). Life expectancy was found to be lowest in *U. compositae* followed by *R. maidis*, *H. coriandri*, *M. persicae*, *A. pisum*, *R. padi*, *B. brassicae*, *H. setariae* and *C. silvestri.* Life expectancy data revealed that the total lifespan of *A. cardoni* larvae in terms of development was lowest when fed on *U. compositae*, *R. maidis*, *H. coriandri*, and *M. persicae*, and highest when fed on *C. silvestri* and *H. setariae.*

(b) Stage-specific life table

The stage-specific survival was highest on *R. maidis* and lowest on *C. silvestri* (Table 2). Apparent mortality and real mortality were lowest on *R. maidis* and highest on *C. silvestri.* However, the mortality values for '*K*' were lowest and equal both for *U. compositae* and *R. maidis.* It was highest for *C. silvestri.*

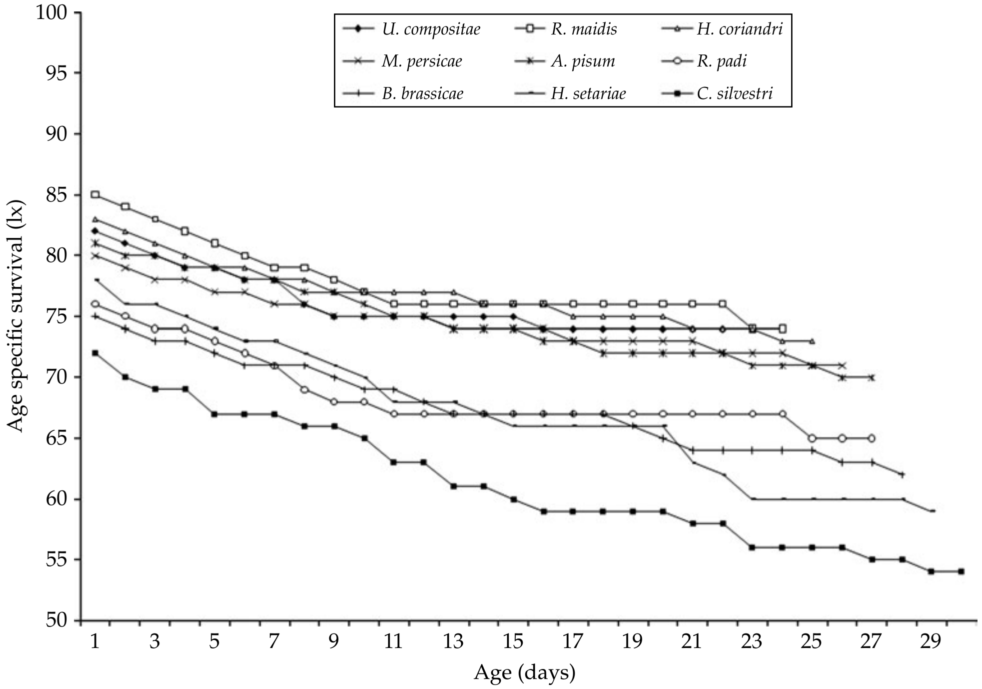

Fig. 2. Age-specific survival (*lx*) of *Anegleis cardoni* (from egg hatch to adult emergence), fed on different aphid species

The MSR for the egg stage was lowest on *R. maidis* and highest when the parents were fed on *C. silvestri.* In the case of larval instars, MSR was found to be zero for the fourth instars on many aphid species (except *H. coriandri*, *H. setariae,* and *C. silvestri*). IM at the egg stage was lowest on *R. maidis* and highest on *R. padi.* For larval instars IM was lowest for fourth instar (except *H. coriandri*).

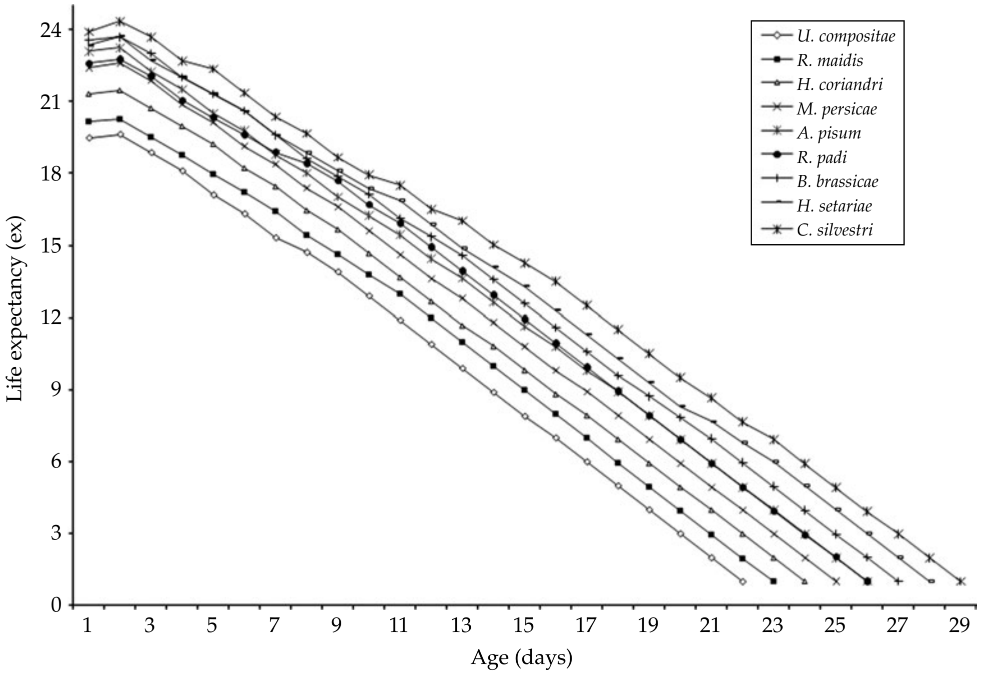

Fig. 3. Age-specific life expectancy (*ex*) of *Anegleis cardoni* (from egg hatch to adult emergence), fed on different aphid species

Table 2. Stage-specific life table of *Anegleis cardoni*, fed on different aphid species

X	l_x	d_x	100 q_x	100 r_x	S_x	k value	MSR	IM
U. compositae								
Egg	100.00	18.00	18.00	18.00	0.82	0.09	0.18	13.32
Instars								
I	82.00	3.00	3.66	3.00	0.96	0.02	0.04	2.71
II	79.00	3.00	3.80	3.00	0.96	0.02	0.04	2.81
III	76.00	1.00	1.32	1.00	0.99	0.01	0.01	0.97
IV	75.00	1.00	0.00	0.00	1.00	0.00	0.00	0.00
Pre-pupa	75.00	1.00	1.33	1.00	0.99	0.01	0.01	0.99
Pupa	74.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
Emergence	74.00	$\kappa = 0.131$						
R. maidis								
Egg	100.00	14.00	14.00	14.00	0.86	0.07	0.14	10.36
Instars								
I	86.00	4.00	4.65	4.00	0.95	0.02	0.05	3.44
II	82.00	3.00	3.66	3.00	0.96	0.02	0.04	2.71
III	79.00	3.00	3.80	3.00	0.96	0.02	0.04	2.81
IV	76.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
Pre-pupa	76.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
Pupa	76.00	2.00	2.63	2.00	0.97	0.01	0.03	1.95
Emergence	74.00	$\kappa = 0.131$						
H. coriandri								
Egg	100.00	16.00	16.00	16.00	0.84	0.08	0.16	11.68
Instars								
I	84.00	3.00	3.57	3.00	0.96	0.02	0.04	2.61
II	81.00	3.00	3.70	3.00	0.96	0.02	0.04	2.70
III	78.00	1.00	1.28	1.00	0.99	0.01	0.01	0.94
IV	77.00	1.00	1.30	1.00	0.99	0.01	0.01	0.95
Pre-pupa	76.00	1.00	1.32	1.00	0.99	0.01	0.01	0.96
Pupa	75.00	2.00	2.67	2.00	0.97	0.01	0.03	1.95
Emergence	73.00	$\kappa = 0.137$						
M. persicae								
Egg	100.00	2.000	20.00	20.00	0.80	0.10	0.20	14.20
Instars								
I	80.00	3.00	3.75	3.00	0.96	0.02	0.04	2.66
II	77.00	2.00	2.60	2.00	0.97	0.01	0.03	1.84
III	75.00	1.00	1.33	1.00	0.99	0.01	0.01	0.95
IV	74.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
Pre-pupa	74.00	1.00	1.35	1.00	0.99	0.01	0.01	0.96
Pupa	73.00	2.00	2.74	2.00	0.97	0.01	0.03	1.95
Emergence	71.00	$\kappa = 0.149$						
A. pisum								
Egg	100.00	19.00	19.00	19.00	0.81	0.09	0.19	13.30
Instars								
I	81.00	3.00	3.70	3.00	0.96	0.02	0.04	2.59
II	78.00	3.00	3.85	3.00	0.96	0.02	0.04	2.69
III	75.00	2.00	2.67	2.00	0.97	0.01	0.03	1.87
IV	73.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
Pre-pupa	73.00	1.00	1.37	1.00	0.99	0.01	0.01	0.01
Pupa	72.00	2.00	2.78	2.00	0.97	0.01	0.03	1.94
Emergence	70.00	$\kappa = 0.155$						
R. padi								
Egg	100.00	24.00	24.00	24.00	0.76	0.12	0.24	15.60
Instars								
I	76.00	4.00	5.26	4.00	0.95	0.02	0.05	3.42
II	72.00	4.00	5.56	4.00	0.94	0.02	0.06	3.61
III	68.00	1.00	1.47	1.00	0.99	0.01	0.01	0.96
IV	67.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00

Table 2. *(continued).*

X	l_x	d_x	100 q_x	100 r_x	S_x	*k* value	MSR	IM
Pre-pupa	67.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
Pupa	67.00	2.00	2.99	2.00	0.97	0.01	0.03	1.94
Emergence	65.00	$\kappa = 0.187$						
B. brassicae								
Egg	100.00	25.00	25.00	25.00	0.75	0.12	0.25	15.50
Instars								
I	75.00	4.00	5.33	4.00	0.95	0.02	0.05	3.31
II	71.00	2.00	2.82	2.00	0.97	0.01	0.03	1.75
III	69.00	2.00	2.90	2.00	0.97	0.01	0.03	1.80
IV	67.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
Pre-pupa	67.00	2.00	2.99	2.00	0.97	0.01	0.03	1.85
Pupa	65.00	3.00	4.62	3.00	0.95	0.02	0.05	2.86
Emergence	62.00	$\kappa = 0.208$						
H. setariae								
Egg	100.00	22.00	22.00	22.00	0.78	0.11	0.22	12.98
Instars								
I	78.00	5.00	6.41	5.00	0.94	0.03	0.06	3.78
II	73.00	4.00	5.48	4.00	0.95	0.02	0.05	3.23
III	69.00	2.00	2.90	2.00	0.97	0.01	0.03	1.71
IV	67.00	1.00	1.49	1.00	0.99	0.01	0.01	0.88
Pre-pupa	66.00	3.00	4.55	3.00	0.95	0.02	0.05	2.68
Pupa	63.00	4.00	6.35	4.00	0.94	0.03	0.06	3.75
Emergence	59.00	$\kappa = 0.229$						
C. silvestri								
Egg	100.00	28.00	28.00	28.00	0.72	0.14	0.28	15.12
Instars								
I	72.00	4.00	5.56	4.00	0.94	0.02	0.06	3.00
II	68.00	4.00	5.88	4.00	0.94	0.03	0.06	3.18
III	64.00	3.00	4.69	3.00	0.95	0.02	0.05	2.53
IV	61.00	2.00	3.28	2.00	0.97	0.01	0.03	1.77
Pre-pupa	59.00	1.00	1.69	1.00	0.98	0.01	0.02	0.92
Pupa	58.00	4.00	6.90	4.00	0.93	0.03	0.07	3.72
Emergence	54.00	$\kappa = 0.268$						

MSR, mortality: survivor ratio; IM, indispensable mortality.

The overall mortality prior to the adult stage of *A. cardoni* was lowest on *U. compositae, R. maidis, H. coriandri* and *M. persicae*, while it was highest when fed on *C. silvestri* and *H. setariae* (Table 3). The first instars suffered the highest mortality regardless of the aphid species fed.

Discussion

Our results revealed that *A. cardoni* successfully fed on the different aphid species provided, except *A. nerii*. Each aphid species significantly influenced the various developmental attributes of *A. cardoni*, with certain species being more suitable than others. Mortality life table data revealed *R. maidis* as the most suitable aphid prey. However, the overall percentage of mortality did not differ between *U. compositae* and *R. maidis.* The developmental parameters, *viz.* the percentage of immature survival, adult weight, development rate and growth index was highest in *U. compositae.* Therefore, on the basis of the different parameters studied, *U. compositae* may be considered as the most suitable and *C. silvestri* as the least suitable aphid prey for the mass production of *A. cardoni*.

The lesser suitability of prey may be because of lower nutrient quality or lower palatability (Hodek, 1993). Variations in lipid and carbohydrate content are known to influence the various life attributes of the predator (Fischer *et al.*, 2004; Ziegler and Van Antwerpen, 2006). This can be a result of nutritional variability in aphids, which may be host plant derived. Phytophagous insects are also known to select plants on the basis of nutritional content (Price, 1997), causing significant influence on herbivores and in turn their predator's performance in terms of development and survival. The presence of nutritional phagostimulants (such as carbon and nitrogen) as well as defensive metabolites that directly affect the potential and survival rate of the

Table 3. Percentage mortality in immature stages of *Anegleis cardoni*, fed on different aphid species

Aphid species	Stage				
	First instar (%)	Second instar (%)	Third instar (%)	Fourth instar (%)	Overall mortality prior to adult stage (%)
U. compositae	37.50	37.50	12.50	0.00	26.00
R. maidis	40.00	30.00	30.00	0.00	26.00
H. coriandri	33.33	33.33	11.11	11.11	27.00
M. persicae	42.86	28.57	14.29	0.00	29.00
A. pisum	33.33	33.33	22.22	0.00	30.00
R. padi	44.44	44.44	11.11	0.00	35.00
B. brassicae	40.00	20.00	20.00	0.00	38.00
H. setariae	33.33	26.67	13.33	6.67	41.00
C. silvestri	28.57	28.57	21.43	14.29	46.00

predator may play a role in this (Awmack and Leather, 2002; Sarfraz *et al.*, 2006). Such an influence of the different host plants on the suitability of an aphid *A. craccivora* to the green lacewing *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) has been reported (Balasubramani and Swamiappan, 1998). Even for the ladybird *Hippodamia variegata* Goeze (Coleoptera: Coccinellidae), the suitability of *A. gossypii* from different host plants has also been reported (Wu *et al.*, 2010), indicating that host plants significantly affect the ladybird's life attributes. The poor performance of *A. cardoni* fed on *A. nerii* may be attributed to the presence of some host plant-derived toxic substances, such as alkaloids, cardinolides and proteolytic enzymes (Seiber *et al.*, 1982; Morsy *et al.*, 2001). These substances have been reported to have larvicidal properties. Under controlled conditions, fractions from latex of *C. procera* (R. Br.) (Asclepiadaceae) were responsible for mortality in most of the first instars before reaching second instars in *Aedes aegypti* (Linnaeus) (Diptera: Culicidae) (Ramos *et al.*, 2006). In another study, chemical extracts from *C. procera* caused feeding repellence and increased larval and pupal mortality in *Henosepilachna elaterii* (Rossi) (Coleoptera: Coccinellidae) (Ahmed *et al.*, 2006). Some predatory ladybird beetles have been found to feed directly on the prey's host plant tissue, which influenced their growth and development (Moser *et al.*, 2008), although this was not observed in the present study.

Other than nutrition, prey suitability is also influenced by many factors, such as prey quantity (Dixon and Guo, 1993; Omkar *et al.*, 2010), sex (Selander, 1966), age (Sandlin and Willig, 1993), and the size of the prey and the predator (Zerba and Collins, 1992), spatial location of the prey (Murdoch *et al.*, 1975) and also the chance encounters between prey and predator (Sherratt and Macdougall, 1995). However, in the current study, higher immature survival, shorter developmental durations and lower overall mortality of *A. cardoni* fed on *U. compositae* may be attributed to the smaller size of this aphid in comparison with other aphid species. Studies have shown that the capture rate decreases with an increase in size of the prey because better defence responses in larger prey promote a better chance to escape (Chau and Mackauer, 1997). However, according to the optimal foraging theory, predators maximize their energy returns by consuming large prey (Schoener, 1969). Thus even if the costs associated with consuming small and large prey are different, both could result in a lower net energy gain than with intermediate-sized prey (Roger *et al.*, 2001).

Low overall mortality found in *U. compositae*, *R. maidis*, *H. coriandri* and *M. persicae* in comparison with other aphid species indicates these aphids to be nutritionally more suitable for *A. cardoni.* Differences in mortality values may also be attributed to the difference in prey mobility, as a less mobile prey is easier to predate upon and consume. Mobility and vigour increase with size, which enhances the efficiency of defensive strategies of prey against predators (Evans, 1976). Differences in tegument characteristics of the prey also influence the predation rate of the predator, because prey with penetrable covers are more likely to be captured and consumed than those with thick covers (Honda and Luck, 1995).

The higher mortality of the lower instars could be due to the difficulty in capturing prey, thereby reducing nutritional access (Dixon, 1959) and also their own thinner cuticles and smaller sizes, which increase their vulnerability to prey. In the current study, the curve drawn for life expectancy of immature stages of *A. cardoni* up to adult emergence showed low peaks when fed on *U. compositae* in comparison with the other tested aphid species. This indicates that individuals having lower development durations will show lower life expectancy. As in the case of *Scymnus subvillosus*

(Goeze) (Coleoptera: Coccinellidae), a lower development period with lower life expectancy and higher development period with higher life expectancy was reported (Atlihan and Chi, 2008).

Earlier, the development of *A. cardoni* was investigated on three aphid species, *viz. A. gossypii*, *A. craccivora* and *L. erysimi*. The development of all immature stages of *A. cardoni* was fastest on *A. gossypii* than on the other aphid species including those tested in the current study. Therefore, *A. gossypii* may be considered as the most suitable aphid for this ladybird. Also, the development of the ladybird on *A. craccivora* was faster than on *B. brassicae, H. setariae, C. silvestri* and *A. nerii* and that on *L. erysimi* was faster than on *H. setariae, C. silvestri* and *A. nerii* (Omkar *et al.*, 2009).

Thus the study concludes that each of the ten tested aphid species has a significant influence on the growth, development and survival of *A. cardoni. Aphis nerii* may be considered as toxic prey, since no larva of *A. cardoni* succeeded in developing to the adult stage when fed on it. Developmental durations, percentage of survival, adult weight, growth index and generation survival of immature stages of *A. cardoni* were highest when fed on *U. compositae*, *R. maidis*, *H. coriandri* and *M. persicae* in comparison with the other aphid species tested. Hence these aphids may be considered as the most suitable prey, and *H. setariae* and *C. silvestri* as the least suitable prey. The suitability of aphid species in decreasing order was: *U. compositae* > *R. maidis* > *H. coriandri* > *M. persicae* > *A. pisum* > *R. padi* > *B. brassicae* > *H. setariae* > *C. silvestri* > *A. nerii.* Therefore, it can be clearly inferred that rearing of immature stages of *A. cardoni* on *U. compositae*, *R. maidis*, *H. coriandri* or *M. persicae* will result in higher production and mass multiplication for better pest management strategies.

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