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Preference–performance of a generalist predatory ladybird: A laboratory study

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Abstract

The fitness consequences of feeding on different aphids, viz. *Aphis craccivora*, *Aphis gossypii*, *Aphis nerii*, *Lipaphis erysimi*, *Myzus persicae*, *Rhopalosiphum maidis*, and *Uroleucon compositae* (Homoptera: Aphididae), for the life stages of a generalist predatory ladybird, *Propylea dissecta* (Coleoptera: Coccinellidae) were measured in the laboratory in terms of their preference (prey biomass consumed and oviposition site selection), performance (development, survival, reproduction, mortality and fertility life tables, and individual fitness levels of predator), and preference–performance correlations. The study revealed that *P. dissecta* consumed *A. craccivora* the most and deposited more eggs on plants infested with this aphid species. The performance levels of predator varied significantly between aphid species with best performance on *A. craccivora* and worst on *A. nerii*. High performance on *A. craccivora* was contradictory to most literature and can be attributed to host plant dependent prey suitability. *P. dissecta* seems to be a generalist aphidophagous ladybird as it readily developed and reproduced on all seven aphid species. We correlated a composite performance measure (individual fitness) to two estimates of preference (biomass of prey consumed and oviposition site selection). Positive preference–performance correlations suggest that preferential prey consumption and selection of a host plant–prey complex as an oviposition site are an indicator of ladybird performance.

Keywords: *Propylea dissecta*; Coccinellidae; Feeding specialization; Ladybird; Preference; Performance; Preference–performance correlation

1. Introduction

Food associations of ladybirds (Coleoptera: Coccinellidae) have been put under detailed scrutiny because of their economic value as biocontrol agents. Earlier, the presence of a ladybird in prey vicinity was sufficient to warrant its inclusion in prey range of predator (Balduf, 1935; Schilder and Schilder, 1928). Thompson (1951), however, challenged this view and stated that identification of prey range needs to be based on more concrete proofs, such as the life attributes on a particular prey. Mills (1981) suggested that the presence of ladybird larvae, particularly later instars, in prey colonies is an indicator of essential or nursery (prey preferred by immature stages) prey. It was on further extension of the above concept that the classifications of prey based on survival, development, and reproduction of predator, cost of capture, and toxin content were brought forward, and are the largely accepted means of identifying prey range (Hodek, 1959, 1962; Hodek and Honek, 1996; Malcolm, 1992). The presence of a hierarchy among different prey and specialization for certain prey has been proved for a number of ladybird species (Blackman, 1965, 1967; Kalushkov, 1994, 1998; Mills, 1981; Olszak, 1986; Omkar and Bind, 2004; Omkar and James, 2004; Omkar and Srivastava, 2003; Pervez and Omkar, 2004a). The costs and benefits of prey specialization have recently been studied and have indicated increasingly better performance of the predator on a poor aphid when reared continuously over six

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generations (Rana et al., 2002). Another study however discussed the impact of mixed diets on life attributes of predator and the better performance on them owing to innate dietary self-selection (Soares et al., 2004).

Prey suitability and preference are subjected to a number of factors, such as host plant constituents, plant architecture, and seasons (Clark and Messina, 1998; Geitzenauer and Bernays, 1996; Hukusima and Kamei, 1970; Krebs and McCleery, 1994; Okamoto, 1966; Vohland, 1996). The foraging behaviour of adult females among available food types, i.e., preference, and the subsequent development, survival, and reproduction, i.e. performance, are important determinants of prey suitability (Tauber and Tauber, 1987). Preference and performance correlations have largely been studied in herbivorous insects (as reviewed by Thompson, 1988; Via, 1986) but very few in predaceous ones (Sadeghi, 2002; Sadeghi and Gilbert, 2000).

Propylea dissecta (Mulsant) (Coleoptera: Coccinellidae) is a polymorphic, Oriental ladybird commonly found in the agricultural fields infested with *Aphis gossypii* and *A. craccivora* (Pervez and Omkar, 2004a). It has earlier been reported from aphids, *Aphis affinis* del Guercio and *Myzus persicae* (Sulzer) (Singh and Bali, 1993), and coconut caterpillar *Opsinia arenosella* Walker (Pillai and Nair, 1986). Though the growth, development, and reproduction of its pale morph on seven aphid species have been studied (Pervez and Omkar, 2004a), that of the typical morph has not yet been studied. Furthermore, no a priori studies on its preference–performance correlations exist. Fitness consequences of seven aphid species commonly occurring in the local habitat of *P. dissecta* on its various life attributes, viz. development, reproduction, fertility and mortality life tables, and individual fitness levels are thus being assessed here.

The study reported here has three aims. First, we aim to identify the preference of typical morph of *P. dissecta* for host plant–aphid complexes present commonly in its local habitat by studying the biomass of prey consumed and oviposition site selection. Second, we aim to assess the performance of the ladybird by comparing the fitness consequences (intrinsic suitability) of the different aphid species as food for its larvae and adults under laboratory conditions, testing the null hypothesis that all aphids are equally good as food for the larvae. Third, we test the existence of a preference–performance correlation in *P. dissecta*, i.e., whether preference is indicative of the performance of this ladybird on a prey.

2. Materials and methods

2.1. Laboratory maintenance

A laboratory culture of *P. dissecta* was established from adults captured in the fields adjoining the city of Lucknow, India, and kept at 25 ± 2 °C, 65 ± 5% RH and 14L:10D on a mono-specific aphid supply in Petri dishes (9.0 × 2.0 cm). The following aphid–host plant complexes were chosen for their local availability: *A. craccivora* Koch from bean (*Dolichos lablab* Linnaeus), *A. gossypii* Glover from bottle gourd (*Lagenaria vulgaris* Seringe), *Aphis nerii* Boyer de Fonsclombe from milkweed (*Calotropis procera* (Aiton)), *Lipaphis erysimi* (Kaltenbach) from mustard (*Brassica campestris* Linnaeus), *M. persicae* from black nightshade (*Solanum nigrum* Linnaeus), *Rhopalosiphum maidis* (Fitch) from sorghum (*Sorghum bicolor* (Linnaeus)), and *Uroleucon compositae* (Theobald) from safflower (*Carthamus tinctorius* Linnaeus). The field-collected adults were supplied exclusively with either one of the aphids for one generation and the resultant F_1 adults were used in the experiments. Fresh aphids were provided ad libitum every 24 h.

Rearing of adults and their progeny for a generation on an exclusive aphid supply prior to being used in experiments was done to acclimatise them to the prey, and avoid loss of fitness of future generations from a sudden switch from one nutrient source to another (field prey to laboratory prey) as indicated by Rana et al. (2002). All experiments were conducted under abiotic conditions similar to that of the stock culture.

3. Experimental design

3.1. Preference

3.1.1. Prey biomass consumption

A 24 h starved adult female (10-day-old) was provided with 100 aphids of either one of the seven aphids on respective host plant twig in a muslin-covered beaker (9.5 cm × 6.5 cm) for 3 h after which the unconsumed aphids were counted. The experiment was conducted in 10 replicates for each of the seven aphids.

Second instars of the larger sized aphids, *A. craccivora* and *A. nerii*, and third instar of smaller sized aphids, viz. *A. gossypii*, *L. erysimi*, *M. persicae*, *R. maidis*, and *U. compositae*, were selected to standardise size of prey across the seven different prey types. The second and third instar stages were selected to ensure intermediate size for maximum prey biomass utilisation and consumption (Roger et al., 2000). The biomass consumption was evaluated by weighing 100 aphids of each species (instars as provided in experiment) using electronic balance (SARTORIUS-H51, Westbury, New York, USA) from which average biomass of prey consumed by each individual was calculated and the data were subjected to one-way ANOVA followed by post hoc Tukey's test of comparison using MINITAB (2003) on PC.

3.1.2. Oviposition site selection

The ovipositional behaviour of *P. dissecta* was evaluated on seven host plant–aphid combinations under choice conditions to decipher its preference for oviposition site. The experiment was conducted in a rectangular glass chamber (70 × 50 × 3 cm), which was divided equally into 8 chambers (17.5 × 25 × 3 cm). One of the corner chambers was sealed off using thermocol to prevent entry of ladybirds or aphids into it. All the borders of the remaining seven chambers were lined with 1 in. double adhesive tape and a host plant–aphid combination placed in the centre of each one of the chambers. The adhesive on the tape was strong enough to prevent the migration of aphids but did not dissuade the ladybirds from moving between chambers.

Once the aphid–host plant combinations were positioned, 10 mated and ovipositing adult females (10-day-old) were released in the centre of the arena, and allowed to move around freely. After 24 h, the females were removed and the number of eggs laid in the chambers was counted to determine the preference for oviposition site. The experiment was replicated five times. The data were subjected to one-way ANOVA and post hoc Tukey's test of comparison.

3.2. Performance

3.2.1. Pre-adult development and immature survival

Larval performance depends on food quality and mortality due to natural enemies, with the latter being almost minimised in laboratory rearing conditions. Thus, only the effect of prey quality (nursery food in this case) on performance of the instars was studied.

Five eggs laid by F_1 females were collected from stock and observed for hatching. The incubation period was recorded and hatched first instars transferred to glass beaker (9.5 × 6.5 cm). Maximum of five larvae was placed in a beaker constituting a replicate. The experiment was replicated 10 times. Each larva received a mono-specific aphid supply similar to that provided to the parental generation in stock. The supply of aphids was refreshed every 24 h and increased as needed, to keep pace with the requirements of the larvae; ad libitum supply of aphids but in equal amounts between species was provided. Time taken to moult into next instar and number of larvae surviving each instar was recorded. Prepupal and pupal periods, and number of pupae formed were also recorded. Since there were five larvae per replicate, the mean values per replicate were used for analysis. Percent immature survival and percent adult emergence (no. of adults × 100/no. of pupae) were calculated.

The data were subjected to one-way ANOVA using statistical software MINITAB (2003). Differences between means of activity were calculated using post hoc Tukey's honest significance test at 5% levels. Data on percent immature survival and adult emergence were transformed using arcsine square root transformation prior to being subjected to ANOVA. All data were tested for normality using Bartlett's test (SAS, 2002).

3.2.2. Mortality life table

For the construction of mortality life table, the following parameters, viz. x is the age interval at which sample was taken, i.e., eggs, the four larval instars, prepupae, pupae, and adults in the present study; S_x is the survival rate of a stage, calculated as number of individuals surviving stage x/number of individuals in $x-1$ (preceding stage); k value is a dimensionless measure of the mortality within age interval x calculated as the differences between log values of number of surviving individuals in subsequent stages; and κ (kappa) is the sum of k values, were calculated from the observations of Section 3.2.1 (Morris and Miller, 1954). Generation survival was calculated as the number of daughter females/initial number of eggs (Harcourt, 1969).

3.2.3. Reproduction

For the assessment of reproductive performance of *P. dissecta* on seven aphid species, 10 pairs of newly emerged adults obtained from Section 3.2.1 were kept in Petri dishes for lifetime (one pair per Petri dish constituting a replicate, thus, a total of 10 replicates) and fed the same prey on which they were reared as larvae and in the stock. One pair was taken from each replicate of Section 3.2.1.

Pre-oviposition, oviposition, and post-oviposition periods, daily oviposition, fecundity, and percent egg viability were recorded. Age-specific fecundity in most ladybirds follows a triangular trend also known as triangular fecundity function, i.e. the daily oviposition increases with age until a peak is obtained and then declines on further aging (Dixon, 2000). The variation in the fecundity patterns was studied in terms of day of peak (female age at peak oviposition) and peak oviposition rate (eggs laid at the peak). These parameters were selected for analysis as they help provide statistical interpretation of changes in age-specific fecundity trends with variation in food consumed. All data were subjected to one-way ANOVA and comparisons among means using post hoc Tukey's honest significance test at 5% levels (MINITAB, 2003).

3.2.4. Fertility life table

Demographic fertility life table parameters, viz., net reproductive rate ($R_0 = \sum l_x m_x$), mean generation time ($T_c = \sum x l_x m_x / R_0$), intrinsic rate of increase ($r_m = \ln R_0/T_c$), finite rate of increase ($\lambda = e^{r_m}$; $e = 2.718228$), and doubling time (DT) = ln ($2/r_m$) were calculated (Andrewartha and Birch, 1954; Birch, 1948) from observations of Section 3.2.3, and the data on the number of females resulting from the total fecundity of Section 3.2.3.

In the calculations, $x =$ age since emergence, $l_x =$ number of females surviving in a given proportion on a particular aphid, and $m_x =$ net fecundity of an emerging female on a particular aphid.

3.2.5. Individual fitness

Most studies on suitability of abiotic and biotic conditions deal with different aspects of growth, development, and reproduction in isolation. Therefore, an individual fitness measure (r) for each of the 10 females from Section 3.2.3 was calculated as a composite performance measure (McGraw and Caswell, 1996) as $r = [\ln(mV)]/D$, where m is the survival (1 or 0), V is the potential fecundity, and D is the total developmental time. The fitness was subjected to one-way ANOVA and post hoc Tukey's test for comparison of means at 5% levels (MINITAB, 2003).

3.3. Preference–performance correlation

The individual fitness levels were considered as a composite performance measure and correlated (MINITAB, 2003) with two preference measures, viz. prey biomass consumed and oviposition site selection, to obtain the preference–performance correlation. Performance was also regressed linearly against the two preference measures (MINITAB, 2003).

4. Results

4.1. Preference

4.1.1. Prey consumption

There was a significant difference in the consumed biomass of seven aphid species ($P < 0.001$; Table 1). Based on prey consumption, the order of aphid species was *A. craccivora* > *A. gossypii* > *U. compositae* > *R. maidis* > *L. erysimi* = *M. persicae* > *A. nerii* (Table 1).

4.1.2. Oviposition site selection

The results reveal that females of *P. dissecta* preferentially oviposited in the vicinity of *A. craccivora* (64.90 ± 8.73 eggs) followed by *A. gossypii* (53.40 ± 11.84 eggs), *U. compositae* (27.60 ± 6.31 eggs), *R. maidis* (19.60 ± 2.20 eggs), *L. erysimi* (11.60 ± 1.75 eggs), *M. persicae* (9.80 ± 1.66 eggs), and *A. nerii* (2.20 ± 1.02 eggs). An overall significant difference in preferential ovipositional site selection was observed ($F = 60.29$; $P < 0.001$; $df = 4, 30$). Comparison of means revealed significant differences among the aphid species except between *M. persicae* and *L. erysimi*. Thus, the rank-order hierarchy based on site selection of *P. dissecta* was *A. craccivora* > *A. gossypii* > *U. compositae* > *R. maidis* > *L. erysimi* = *M. persicae* > *A. nerii*.

4.2. Performance

4.2.1. Pre-adult development and immature survival

The data (Table 1) revealed that when fed seven aphid species, total developmental period of immature stages of *P. dissecta* was shortest on *A. craccivora* and longest on *A. nerii*, and the differences in individual means were statistically significant among all aphid species except for those between *U. compositae* and *R. maidis*. The percent immature survival and adult emergence were least on *A. nerii*. There were no significant differences in the immature survival among *A. craccivora*, *A. gossypii*, *U. compositae*, and *R. maidis* while, adult emergence did not significantly differ between *A. craccivora* and *A. gossypii*.

4.2.2. Mortality life table

Survival rates (Sx) were lowest for eggs followed by pupae and first instars (Fig. 1). Kappa values of immature stages reared on *A. craccivora* were lowest, while they were highest for those reared on *A. nerii*. Generation survival was highest when immature stages were reared on *A. craccivora* and lowest when fed *A. nerii* (Table 1). On certain occasions, the larvae (three on *A.*

Table 1
Developmental parameters of *P. dissecta* when fed on seven aphid species

Aphid	Biomass of aphids consumed (mg)	Total development period (days)	Larval survival (%)	Adult emergence (%)	Kappa values	Generation survival
Ac	16.84 ± 1.64^{f}	14.24 ± 0.28^{a}	97.56 ± 3.43^{c}	98.93 ± 2.34^{e}	0.0297	0.47
Ag	13.64 ± 0.77^{e}	15.04 ± 0.17^{b}	95.78 ± 3.66^{c}	94.46 ± 4.93^{e}	0.0757	0.44
Uc	10.61 ± 0.99^{d}	15.32 ± 0.23^{c}	91.81 ± 3.37^{c}	91.73 ± 3.59^{d}	0.1215	0.39
Rm	8.58 ± 7.84^{c}	15.57 ± 0.17^{c}	$89.84 \pm 4.41^{b,c}$	88.30 ± 8.51^{c}	0.1624	0.38
Le	7.84 ± 0.95^{b}	16.13 ± 0.11^{d}	83.89 ± 6.19^{b}	83.09 ± 5.69^{b}	0.2596	0.32
Mp	7.53 ± 1.05^{b}	18.62 ± 0.24^{e}	83.82 ± 3.27^{b}	82.83 ± 8.44^{b}	0.3449	0.27
An	5.22 ± 1.12^{a}	20.11 ± 0.31^{f}	78.63 ± 5.29^{a}	73.22 ± 9.90^{a}	0.5498	0.17
F value	62.34	870.61	25.20	16.34		

Values are means ± SD; F values significant at $P < 0.001$; Tukey's test range = 4.31; $df = 6, 63$. Values followed by same alphabets indicate no significant differences. Ac, Ag, Uc, Rm, Le, Mp, and An stand for *A. craccivora*, *A. gossypii*, *U. compositae*, *R. maidis*, *L. erysimi*, *M. persicae*, and *A. nerii*, respectively.

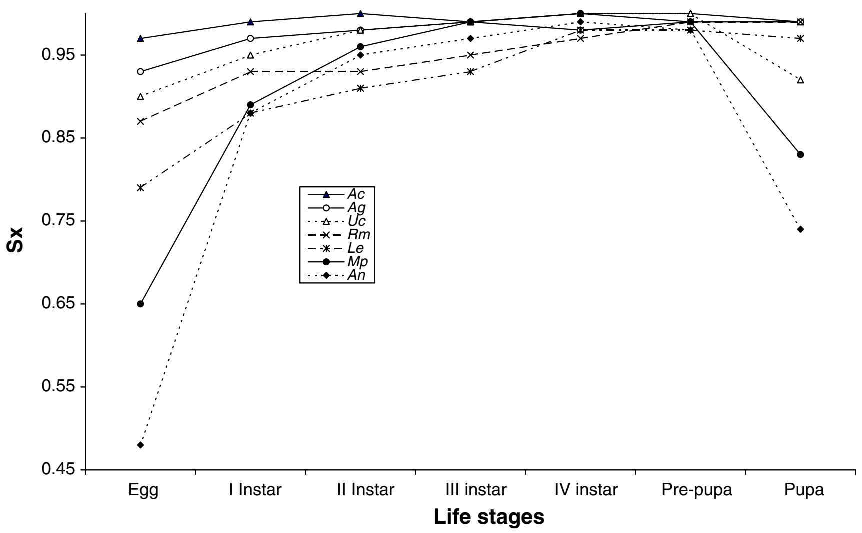

Fig. 1. Survial rates (Sx) of development stages of *P. dissecta* when fed on different prey species Ac, Ag, Uc, Rm, Le, Mp, and An stand for *A. craccivora*, *A. gossypii*, *U. compositae*, *R. maidis*, *L. erysimi*, *M. persicae*, and *A. nerii*, respectively.

gossypii, six on *R. maidis*, and four on *A. nerii*) were found entangled in webs of spiders that had entered the beakers in the folds of host plant twig. On one occasion, two second-instar larvae were consumed by ants (*Formosa rufa*) that had entered a beaker with *A. gossypii*. These accidental deaths due to heterospecific predation were not included during analysis of data.

4.2.3. Reproduction

The pre-oviposition, oviposition, and post-oviposition periods, fecundity and percent egg viability varied significantly when adults of *P. dissecta* were fed on different aphid species (Table 2). Age-specific fecundity was triangular on all aphid species. The peak of oviposition was achieved earliest when *A. craccivora* was used as prey (Fig. 2). This was followed by *A. gossypii*, *U. compositae*, *R. maidis*, and *L. erysimi* with fecundity graphs on the latter three attaining their peak in oviposition at almost the same time. The peak was further delayed in *M. persicae* and *A. nerii*, with latter showing multiple peaks and fluctuations. The ages ($F = 22.98$; $P < 0.001$; $df = 6$, 63) and oviposition rates ($F = 136.88$; $P < 0.001$; $df = 6$, 63) at the peak of fecundity differed significantly with aphid species (Fig. 2).

4.2.4. Fertility life table

Demographic parameters of prey dependent fertility life table revealed that net reproductive rate (R_0), intrinsic rate of increase (r_m), and finite rate of increase (λ) were highest when *A. craccivora* was used as prey, and lowest on *A. nerii* (Table 3). The generation and doubling times were lowest on *A. craccivora*, and highest on *A. nerii*.

4.2.5. Individual fitness

Individual fitness level calculated as a composite statistical performance measure was found to differ significantly with the seven aphid species (Table 2). It was highest on *A. craccivora* and lowest on *A. nerii*.

Table 2
Reproductive attributes of *P. dissecta* when fed on seven aphid species

Aphid	Fecundity	Hatching %	Pre-oviposition period (days)	Oviposition period (days)	Post-oviposition period (days)	Fitness
Ac	941.80 ± 79.02^{f}	94.48 ± 2.56^{d}	4.00 ± 0.94^{a}	45.20 ± 2.44^{e}	6.10 ± 1.10^{b}	0.48 ± 0.01^{g}
Ag	913.90 ± 35.48^{f}	92.53 ± 2.07^{d}	4.60 ± 0.84^{a}	43.30 ± 1.95^{d}	6.60 ± 1.71^{b}	0.45 ± 0.01^{f}
Uc	792.60 ± 27.02^{e}	$89.43 \pm 3.22^{c,d}$	5.60 ± 1.08^{a}	41.30 ± 3.50^{d}	$7.80 \pm 2.04^{b,c}$	0.44 ± 0.01^{e}
Rm	706.20 ± 38.41^{d}	87.25 ± 2.86^{c}	9.60 ± 1.17^{b}	35.30 ± 2.35^{c}	9.40 ± 1.17^{d}	0.42 ± 0.07^{d}
Le	602.90 ± 37.15^{c}	79.09 ± 1.71^{b}	10.50 ± 1.43^{b}	29.10 ± 1.79^{b}	$11.40 \pm 1.30^{c,e}$	0.39 ± 0.04^{c}
Mp	472.10 ± 50.43^{b}	77.35 ± 3.77^{b}	10.60 ± 2.27^{b}	31.40 ± 1.84^{b}	4.30 ± 3.02^{a}	0.33 ± 0.07^{b}
An	153.20 ± 26.57^{a}	63.67 ± 7.00^{a}	13.50 ± 2.55^{c}	25.80 ± 2.97^{a}	5.60 ± 3.63^{a}	0.25 ± 0.08^{a}
F value	373.36	85.711	51.20	92.10	8.28	1108.69

Values are means ± SD; *F* values significant at $P < 0.001$; Tukey's test range = 4.31; $df = 6$, 63. Values followed by different alphabets indicate significant differences. Ac, Ag, Uc, Rm, Le, Mp, and An stand for *A. craccivora*, *A. gossypii*, *U. compositae*, *R. maidis*, *L. erysimi*, *M. persicae*, and *A. nerii*, respectively.

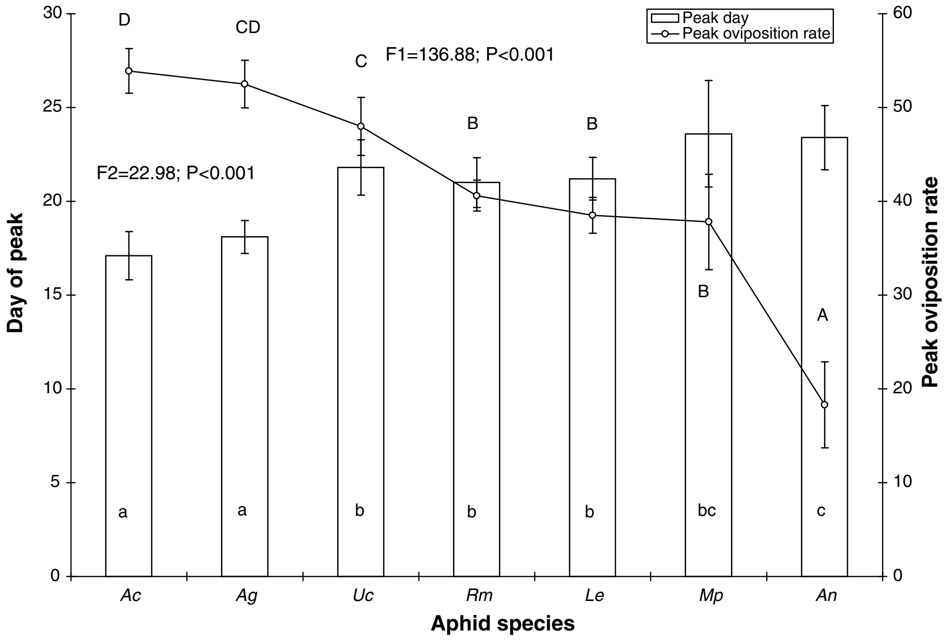

Fig. 2. Graphical representation of shift in peak and peak oviposition rate of *P. dissecta* on different aphid species. Data points are means ± SD; F1 and F2 indicates *F* values of peak oviposition rate and peak day of oviposition, respectively. Points bearing same alphabets indicate no significant differences; upper and lower case alphabets indicate comparison of means of peak oviposition rate and peak day of oviposition, respectively; Ac, Ag, Uc, Rm, Le, Mp, and An stand for *A. craccivora*, *A. gossypii*, *U. compositae*, *R. maidis*, *L. erysimi*, *M. persicae*, and *A. nerii*, respectively.

Table 3
Demographic parameters for *P. dissecta* larvae when raised on seven aphid species

Aphids	R_0	r_m (day^{-1})	T_c (day)	DT (day)	λ (day^{-1})
Ac	475.90	0.27	22.98	2.01	1.31
Ag	470.80	0.25	24.71	2.08	1.28
Uc	412.02	0.24	24.99	2.12	1.27
Rm	388.41	0.21	28.06	2.24	1.18
Le	349.96	0.22	26.60	2.21	1.25
Mp	278.45	0.21	26.69	2.25	1.23
An	93.30	0.17	23.73	2.47	1.18

Ac, Ag, Uc, Rm, Le, Mp, and An stand for *A. craccivora*, *A. gossypii*, *U. compositae*, *R. maidis*, *L. erysimi*, *M. persicae*, and *A. nerii*, respectively. R_0, r_m, T_c, DT, λ, indicate net reproductive rate, intrinsic rate of increase, mean generation time, doubling time, and finite rate of increase, respectively.

4.3. Preference–performance correlation

A strong positive correlation was obtained between oviposition site selection (preference) and fitness levels (performance) ($r = 0.81$; $P < 0.001$). When these two parameters were regressed against each other, the equation $Y = 0.3683X + 18.107$ ($r = 0.76$; $P < 0.001$) was obtained.

The equation, $Y = 0.0126X + 0.3277$ ($r = 0.78$; $P < 0.001$), was obtained when individual fitness levels (performance) were regressed upon biomass of prey consumed (preference). Correlation analysis revealed a prominent positive correlation ($r = 0.84$; $P < 0.001$) between prey consumption and individual fitness levels in adult *P. dissecta*.

On the basis of the above parameters, the order of performance of ladybirds on the seven aphid species was: *A. craccivora* > *A. gossypii* > *U. compositae* > *R. maidis* > *L. erysimi* > *M. persicae* > *A. nerii*.

5. Discussion

The preferential oviposition by *P. dissecta* on certain host plant–aphid complexes indicates a rank-order hierarchy of prey suitability. The finding supports optimal foraging theory, which states that the female is likely to select oviposition sites harbouring prey that will support the development and survival of her progeny (Kindlmann and Dixon, 1993).

Differential biomass consumption is perhaps indicative of aphid palatability and of the ability of ladybirds to show a marked preference. This could be a result of differences in morphology, behaviour, and chemical constitution of aphids (Dixon, 2000; Liepert and Dettner, 1996; Okamoto, 1966). In field conditions, the plant architecture (Clark and Messina, 1998; Vohland, 1996), seasons (Krebs and McCleery, 1994), prey availability, and type (Rana et al., 2002; Sloggett and Majerus, 2000a,b) may modify the prey specificity and the preference of ladybirds. Soares et al. (2004) have recently studied the dietary self-selection behaviour of a ladybird, *Harmonia axyridis* (Pallas), and concluded that a mixed prey diet is more suitable to ladybird than a single prey one. This was probably governed by the innate selection based on physiological status of host plant and aphid performance, nutritional requirements, enzyme equipments, and nutritional budgets required for the development and reproduction of the ladybirds (Dixon, 1998; Klingauf, 1988; Soares et al., 2004).

The increased performance of *P. dissecta* on *A. craccivora* may be attributed to: (1) the presence of suitable nutrient levels in the species, and/or (2) their higher consumption, a probable result of its higher palatability. The high suitability and palatability of *A. craccivora* here are rather interesting, since it were previously reported as toxic for many ladybirds (Azam and Ali, 1970; Hodek, 1960; Hukusima and Kamei, 1970; Okamoto, 1966; Obatake and Suzuki, 1985; Takeda et al., 1964). *H. axyridis* did not develop and died when fed on *A. craccivora* obtained from *Robinia pseudoacacia* Linnaeus (Okamoto, 1966). Azam and Ali (1970) reported *A. craccivora* as lethal for *C. septempunctata* when obtained from *Glycinidia* sp. The larvae of *Semiadalia undecimnotata* Schneider (Hodek, 1960) and *H. axyridis* (Okamoto, 1966) died when *Vicia faba* Linnaeus was the host plant of *A. craccivora*.

With the exception of *A. craccivora* feeding on *Vicia sativa* Linnaeus, *V. faba* or *Vigna catiang* var. *sinensis* Walp, the same prey when obtained from other host plants (*R. pseudoacacia*, *Astragalus sinicus* Linnaeus, *Vicia hirsute* (Linnaeus), *Capsella bursa-pastoris* (Linnaeus), *Cardamine flexuosa* With, *Rorippa palustris* (Linnaeus), and *Hemistepta carthamoides* Kuntze) was highly toxic to ladybirds (Hukusima and Kamei, 1970). The presence of the amines, canvanine and ethanolamine, from both host plant and aphid is probably responsible for toxicity of *A. craccivora* from *R. pseudoaccacia* (Obatake and Suzuki, 1985). Influence of host plant on suitability of prey may provide an explanation for the seasonal suitability of aphids (Takeda et al., 1964). On the contrary, Hodek (1960) reported *A. craccivora* (on *V. faba*) as an essential food for *C. septempunctata*. The same from *D. lablab* was reported suitable for *C. septempunctata* (Omkar and Srivastava, 2003). Larvae and adults of *Propylea japonica* (Thunberg) are resistant to even the detrimental effects of *A. craccivora* from *R. pseudoaccacia* (Hukusima and Kamei, 1970). The high suitability and palatability of *A. craccivora* to *P. dissecta* in the present experiment can probably be attributed to the probable favourable chemical constitution of its host plant, *D. lablab*.

Life table studies indicated that the egg stage was the most influenced by prey species followed by pupal stages and first instars. In a previous life table study on *P. dissecta*, albeit on the pale morph, first instars were found to be most vulnerable, while pupal stages were least susceptible to mortality (Omkar and Pervez, 2004). This difference could perhaps have a relation to the different genotypes of the test organism, the present study dealing with the typical morph, while the previous one dealt with the pale morph of *P. dissecta*. Further, Omkar and Pervez (2004) studied different generations on fluctuating temperatures and prey species in an attempt to duplicate the field conditions in laboratory, while the present study involves specific aphid supply at controlled conditions.

Infertility and cannibalism could probably be responsible for most of egg mortality, cannibalism for that of larvae but the reasons for pupal mortality despite its hard case are unclear. Mortality factors have seemingly a major impact on the group reared on *A. nerii*, while minor on *A. craccivora*. The probable causes of infertility have been attributed in previous studies to improper insemination (Hodek and Honek, 1996) or inbreeding depressions (Morjan et al., 1999). Unviable eggs/trophic eggs are considered an asset in the development of progeny (Dixon, 2000; Hemptinne et al., 2000). The increased pupal mortality in larvae fed aphids of poor quality may be attributed to lack of sufficient nutrients and possible energy for the transformation from larval to adult stages. Parasitoids, reported as the key mortality factors for larval instars (Bind, 1998; James, 2001; Kawauchi, 1984; Kuznetsov, 1987; Srivastava, 2000; Srivastava and Omkar, 2004), were not found in the present study.

Both the reproductive rate and generation time were negatively impacted by the supply of *R. maidis*, *L. erysimi*, *M. persicae*, and *A. nerii* leading to a lower intrinsic rate of increase and longer doubling time, thus indicating the relative unsuitability of these prey. Rearing of ladybird on these prey would increase the cost of mass multiplication. The intrinsic and finite rates of natural increase of the predator were highest on *A. craccivora*, a probable result of the increased rate of metabolic activities.

Increase in adult size with age is supposed to play a role in the shaping of fecundity function (Kozlowski and Wiegert, 1986; Roff, 1992; Stearns, 1992; Ziolko and Kozlowski, 1983). However, in insects where adult size remains constant, the population fecundity function is probably shaped by mortality (Stearns and Koella, 1986). In ladybirds, the individual fecundity function is determined by senescence (Dixon and Agarwala, 2002; Kindlmann et al., 2001). Changes in daily oviposition rate of ladybird with time also follow a triangular pathway, indicating a relationship between reproductive age and daily rate of oviposition. Our results show the triangular form to be dependent on food quality. The peak in oviposition was delayed and reduced when prey of inferior quality was provided. This results in a gradual shift in shape of triangle from right-angled triangle (on *A. craccivora*) to acute triangle (on *A. nerii*) via equilateral (*U. compositae* and *R. maidis*) with decline in prey quality. A temperature dependent shift in age-specific fecundity form has earlier been witnessed (Omkar and Pervez, 2002; Pervez and Omkar, 2004b; Ponsonby and Copland, 1998). The right angle shape at high temperatures has been attributed to accelerated metabolism, which results in higher and earlier peak in egg production, and subsequent faster decline in output than that at low temperatures (Pervez and Omkar, 2004b). Dixon (2000) has discussed that suitable abiotic and biotic conditions will promote early reproduction.

The evaluation and analysis of performance levels in relation to prey preference have been considered a reliable indicator of food suitability (McGraw and Caswell, 1996). Oviposition preference in laboratory and fields, and the presence of immature life stages on prey patches have been considered as reliable preference measures (Mills, 1981; Sadeghi and Gilbert, 2000). Though, many other fitness measures have been proposed (Janz et al., 1994; McGraw and Caswell, 1996; Thompson, 1988), the estimation of individual fitness (r) (using potential fecundity, development time, and survival) has been deemed most suitable for determination of intrinsic suitability of aphids to predatory life stages (Rana et al., 2002; Sadeghi and Gilbert, 2000). The positive correlation between biomass of prey consumed and oviposition site selection with individual fitness levels in this ladybird seems to signify that increased consumption of a particular prey and site of oviposition will be reliable indicators of the performance of the ladybird on aphids.

The results of this study indicate the potential use of the seven aphid species for mass multiplication of *P. dissecta*. They can also be exploited for the biological control of the aphids studied, especially *A. craccivora* and *A. gossypii*. The ladybird performance on *U. compositae* and *R. maidis* indicates it to be a mediocre level biocontrol agent for these aphids. However, though it develops and reproduces on the other three aphid species, its performance does not warrant its use as a biocontrol agent to manage these aphids. The results would also help to improve identification of target prey and thus improve the chances of success in their biological control.

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