Biocontrol Science and Technology

Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713409232

Why do neonates of aphidophagous ladybird beetles preferentially consume conspecific eggs in presence of aphids?

Omkar a; Ahmad Pervez a; A. K. Gupta a
a Ladybird Research Laboratory, Department of Zoology, University of Lucknow, Lucknow, India

Online Publication Date: 01 February 2006

To cite this Article: Omkar, Pervez, Ahmad and Gupta, A. K. (2006) 'Why do neonates of aphidophagous ladybird beetles preferentially consume conspecific eggs in presence of aphids?', Biocontrol Science and Technology, 16:3, 233 - 243
To link to this article: DOI: 10.1080/09583150500335707
URL: http://dx.doi.org/10.1080/09583150500335707
Why do neonates of aphidophagous ladybird beetles preferentially consume conspecific eggs in presence of aphids?

OMKAR, AHMAD PERVEZ, & A. K. GUPTA

Ladybird Research Laboratory, Department of Zoology, University of Lucknow, Lucknow, India

(Received 27 February 2005; returned 29 April 2005; accepted 13 July 2005)

Abstract
The neonates of aphidophagous ladybird beetles, *Propylea dissecta*, *Coccinella transversalis* and *Coelophora saucia* preferentially consumed conspecific eggs in presence of essential aphid prey, *Aphis gossypii*. This preference was strongest in *P. dissecta* and recorded in all density combinations of conspecific eggs and aphids. The neonates of all three species developed faster resulting in heavier second instars with lower mortality when fed on conspecific eggs as compared to mobile or defenceless aphids. In addition, they required less dry biomass of conspecific eggs than that of aphids. These results reveal that neonates are benefitted intrinsically when they feed on conspecific eggs. The neonates of *P. dissecta* exhibited discrimination for more nutritious food, as they contacted and ate conspecific eggs more frequently than aphids as their first meal. This discrimination was not found in *Coccinella transversalis* and *Coelophora saucia* possibly due to their bigger sizes and possible higher energy requirements. Although, the major effect of chemical cues was only noticed in *P. dissecta*, it could be concluded that chemicals (surface and within) of conspecific eggs possibly attract neonates for egg–cannibalism, as both eggs and aphids were consumed in greater numbers when coated with egg extracts. The reverse occurred when eggs and aphids were coated with aphid extracts.

Keywords: *Propylea dissecta*, *Coccinella transversalis*, *Coelophora saucia*, *Aphis gossypii*, *Coccinellidae*, *aphids*, *egg-cannibalism*

Introduction
Egg–cannibalism is a common occurrence in predaceous ladybirds (Coleoptera: Coccinellidae), which could be exploited as biocontrol agents for many phytophagous insect and acarine pests (Hodek & Honek 1996; Dixon 2000; Burgio et al. 2002; Santi et al. 2003). This behaviour provides direct benefits to the cannibal by eliminating competitors and protecting other food resources from depletion. The conspecific eggs of insects are nutritious to the larval stages because of high cholesterol contents (MacDonald et al. 1990). Egg–cannibalism could be highly advantageous to neonates as capture of the first meal is critically important for their survival (Dixon 1959). The
neonates are known to have poor foraging capacity (Hemptinne et al. 1992), low walking speed (Dixon & Agarwala 2002), low efficiency of prey capture (Dixon 2000) and slow turning rates (Ponsonby & Copland 2000) compared to later larval instars and adults. Furthermore, they face difficulty in capturing their first prey and often engage in social feeding, which involves the consumption of an aphid by two or more neonates (Hemptinne et al. 2000). A neonate increases its surviving to next instar by using the aphid kill of another larva. Due to smaller size, neonates are sometimes dragged by larger aphids when in a pursuit (Dixon 2000). Aphidophagous female ladybirds normally lay eggs in clusters (Agarwala & Dixon 1993; Agarwala et al. 1997), with some trophic (i.e., unviable) eggs laid purposefully to provide a first meal to neonates as a part of survival strategy (Dixon 2000; Omkar & Mishra, unpublished data). Thus, the first meal of neonates often results from egg—cannibalism within and between clusters of eggs (Dixon 1959; Dimetry 1974; Mills 1982).

Neonates of *Harmonia axyridis* (Pallas), after feeding on conspecific eggs as their initial diet, developed faster than non-cannibals (Osawa 2002). The neonates of *Propylea dissecta* (Mulsant) and *Coccinella transversalis* Fabricius readily attacked and ate conspecific eggs rather than heterospecific eggs (Omkar et al. 2004). *Coleomegilla maculata lengi* de Geer neonates preferred conspecific eggs over aphids, which resulted in faster development and increased weight (Gagne et al. 2002). A wider understanding is needed of how neonates of other aphidophagous ladybirds would respond when given a choice between conspecific eggs and essential food (Hodek & Honek 1996).

Laboratory experiments were designed to find the preference for eggs or aphids by the neonates of three aphidophagous ladybirds, *P. dissecta C. transversalis, and Coleophora saucia* (Mulsant) using choice tests at three densities of eggs and aphids. A consistent preference for conspecific eggs suggests a possible nutritive advantage, as indicated by a close association between preference and performance (Ohgushi 1995; Omkar & Mishra 2005). Such a preference could be due to the nutritional value and/or vulnerability of eggs. Assuming the former to be true, better performance would be expected on conspecific eggs followed by equal performance on mobile and defenceless aphids. If advantage is due to vulnerability, better performances would be expected on both conspecific eggs and defenceless aphids over mobile aphids. Where both factors, are involved, performances on conspecific eggs would be better than defenceless aphids followed by mobile aphids. Thus, to better understand the reasons for this expected preference for egg—cannibalism, the fitness components (developmental time and weight) of neonates of three ladybird species were compared between defenceless and mobile aphids and conspecific eggs. In addition, it would be interesting to find whether prey mobility may influence prey consumption by neonates.

Chemicals present on the surface and within the eggs attract cannibals and provide protection against heterospecifics (Hemptinne et al. 2000, 2001; Omkar et al. 2004). It is likely that chemicals (whether on surface or within) may be involved in the feeding preferences of neonates. Finally, we undertook preliminary investigations to determine the possible role of chemical cues aiding a neonate in egg—cannibalism.

**Materials and methods**

**Stock maintenance**

Adults of *P. dissecta, C. transversalis* and *C. saucia* were collected from fields of *Lagenaria vulgaris* (Seringe), where they were feeding on the aphid, *Aphis gossypii*
Egg-cannibalism in presence of aphids

Neonate coccinellids were offered conspecific eggs and mobile aphids as food in choice experiments. Only mobile aphids were used in a bid to more closely simulate field condition in small experimental arenas. A single neonate of each of the ladybird species was kept in a Petri dish (9.0 × 2.0 cm) provided with (i) 10 conspecific eggs (0–12 h old) and five aphids, (ii) 10 conspecific eggs (0–12 h old) and 10 aphids, and (iii) five conspecific eggs (0–12 h old) and 10 aphids. Three combinations of densities were used to determine whether preference is consistent in each density combination. The eggs were arranged singly and distributed randomly within Petri dishes. After 24 h, the remaining eggs and aphids were counted to determine the number of each prey consumed. Manly’s preference index (MPI) was calculated for each combination of prey density, and based on the proportion of eggs and aphids consumed (Manly et al. 1972).

\[
MPI = \frac{\ln(r_i/A_i)}{\ln(r_{ii}/A_{ii})}
\]

where \( r_i \) and \( r_{ii} \) is the number of prey types I and II eaten, and \( A_i \) and \( A_{ii} \) is the number of prey types I and II initially present. MPI was used because it takes into account prey depletion during predation experiments (Sherratt & Harvey 1993). The experiment was replicated twenty times (\( n = 20 \)). Counts of eggs and aphids consumed in each combination were compared using the Wilcoxon signed rank on statistical software (SAS 2002). MPIs obtained at different combinations of prey density were subjected to square root transformation and compared by \( t \)-test (SAS 2002).

Effect of egg-cannibalism on fitness components of developing neonates

To determine whether egg-cannibalism is advantageous to ladybird fitness, a newly eclosed first instar of each ladybird species, \( P. dissecta \), \( C. transversalis \) and \( C. saucia \) was reared on a known number of either (i) conspecific eggs (0–12 h old), (ii) mobile aphids, and (iii) defenceless aphids (live aphids frozen for 5 h at \(-10^\circ C\)) in a Petri dish (9.0 × 2.0 cm). Prey mobility was manipulated by the use of both mobile and defenceless aphids to determine if neonates are benefitting in terms of shorter development and increased weight due to less effort expended for the capture of immobile prey (hence lesser energy would be consumed). Prey were replenished daily and the arenas were observed three times per day to record the moult to second instar. Immediately after the moulting, the number of prey consumed, developmental period, mortality and weight of the newly formed second instar was recorded. The experiment was replicated 25 times (\( n = 25 \)). The data on developmental period and weight of the newly formed second instar reared on the above three foods were compared using one-way ANOVA (SAS 2002). Percent mortality was analysed by Chi-square goodness-of-fit test. The dry biomass consumption by each larva was evaluated by weighing (i) 50 aphids, and (ii) 50 eggs of each ladybird species that were dried in an incubator at 60°C.
for 24 h. Thereafter, the average dry biomass per individual of each prey species was multiplied by the number of prey consumed by each coccinellid larva.

To determine the effects of ‘species’ and ‘food’ provided on life-attributes, the data on neonate developmental time, weight and dry biomass consumed were analysed with two-way ANOVA with ‘species’ (three levels) and ‘food’ (three levels) as independent variables (SAS 2002).

First prey contacted and eaten by neonates

The experiments were designed to test whether prey mobility may influence prey consumption. Two different combinations of prey were offered for the first contact and attack by the neonates of the three ladybird species. These were (i) 10 conspecific eggs and 10 mobile aphids, and (ii) 10 conspecific eggs and 10 defenceless aphids, placed in a Petri dish (9.0 × 2.0 cm). Neonate of each ladybird species starved for 6 h, were introduced into separate Petri dishes containing one of the two treatments described above. Observations were made on the first prey contacted and first prey eaten by the neonate. The experiment was replicated 20 times (n = 20) for each ladybird species. The data on percentages of initial eggs and aphids consumed within each treatment were compared using Chi-square test (SAS 2002). The data on percentages of eggs and aphids consumed were also compared between the species using Chi-square test (SAS 2002).

Chemical cues related to preferential egg-cannibalism

Conspecific eggs (10 mg) and aphids (10 mg) were crushed separately in 1.5 mL distilled water to prepare egg and aphid extracts. A neonate of each of the three ladybird species was kept in a Petri dish containing 10 conspecific eggs painted with aphid extract and 10 defenceless aphids painted with egg-extract. The treated eggs and defenceless aphids were alternatively arranged. The interchange of chemical extracts on the eggs and aphids was done to test the possible involvement of these chemicals (both surface and within) in the food discrimination by the neonates. Two control treatments were provided by 10 conspecific eggs painted with egg extract and 10 defenceless aphids, and the other by 10 defenceless aphids painted with aphid extract and 10 conspecific eggs. The two control treatments were made to test whether painting of eggs or aphids with their own extract affects their own chemical properties and thereby affecting the outcome of consumption by the neonates. The experiment was replicated 20 times (n = 20). The data on egg and aphid consumption were compared using the Wilcoxon signed rank test (SAS 2002).

Results

Egg-cannibalism in presence of aphids

The neonates of all three ladybird species had a consistent preference for conspecific eggs rather than aphids. Neonates of P. dissecta consumed significantly more eggs than aphids when the food was provided in a combination of five eggs and 10 aphids (Wilcoxon test: Z = 3.62; P = 0.0001; n = 20), 10 eggs and 10 aphids (Wilcoxon test: Z = 5.15; P = 0.0001; n = 20) and 10 eggs and five aphids (Wilcoxon test: Z = 5.45; P = 0.0001; n = 20; Table I). The Manly preference indices for P. dissecta at different combinations revealed a greater preference for eggs than aphids (Table II).
Neonates of *C. transversalis* consumed more eggs than aphids in combinations of 10 eggs and 10 aphids (Wilcoxon test: $Z = 5.46; P < 0.0001; n = 20$) and 10 eggs and five aphids (Wilcoxon test: $Z = 5.16; P < 0.0001; n = 20$). The consumption difference was not significant at the low egg density (Wilcoxon test: $Z = 1.36; P > 0.05; n = 20$; Table I). MPI for *C. transversalis* at different combinations of prey densities revealed a preference for eggs rather than aphids (Table II).

Neonates of *C. saucia* consumed more eggs than aphids when presented in combinations of 10 eggs and 10 aphids (Wilcoxon test: $Z = 4.51; P < 0.0001; n = 20$) and 10 eggs and five aphids (Wilcoxon test: $Z = 5.51; P < 0.0001; n = 20$). The consumption difference was not significant at the low egg density (Wilcoxon test: $Z = 0.23; P > 0.1; n = 20$; Table I). MPI for *C. saucia* at different combinations of prey densities revealed a greater preference for eggs than aphids (Table II).

**Effect of egg-cannibalism on fitness components of developing neonates**

The developmental time, weight of newly emerged second instars, dry biomass of prey consumed during the first instar, and percent mortality of the three ladybird species, *P. dissecta*, *C. transversalis* and *C. saucia* fed eggs, mobile aphids and defenceless aphids are presented in Table III. The development of neonates of *P. dissecta* ($F = 71.99; P < 0.0001; df = 2, 59$), *C. transversalis* ($F = 104.42; P < 0.0001; df = 2, 72$) and *C. saucia*

<table>
<thead>
<tr>
<th>Combination</th>
<th>Species</th>
<th>Eggs</th>
<th>Aphids</th>
<th>Wilcoxon test</th>
</tr>
</thead>
<tbody>
<tr>
<td>5E+10A</td>
<td></td>
<td>2.05±0.11</td>
<td>1.25±0.16</td>
<td>$Z = 3.62^*$</td>
</tr>
<tr>
<td>10E+10A</td>
<td><em>P. dissecta</em></td>
<td>2.75±0.14</td>
<td>1.15±0.13</td>
<td>$Z = 5.15^*$</td>
</tr>
<tr>
<td>10E+5A</td>
<td></td>
<td>3.00±0.18</td>
<td>0.55±0.13</td>
<td>$Z = 5.45^*$</td>
</tr>
<tr>
<td>5E+10A</td>
<td></td>
<td>2.90±0.27</td>
<td>2.40±0.58</td>
<td>$Z = 1.36; NS$</td>
</tr>
<tr>
<td>10E+10A</td>
<td><em>C. transversalis</em></td>
<td>7.70±0.27</td>
<td>1.50±0.31</td>
<td>$Z = 5.46^*$</td>
</tr>
<tr>
<td>10E+5A</td>
<td></td>
<td>7.30±0.23</td>
<td>1.40±0.32</td>
<td>$Z = 5.16^*$</td>
</tr>
<tr>
<td>5E+10A</td>
<td></td>
<td>2.10±0.19</td>
<td>2.00±0.32</td>
<td>$Z = 0.23; NS$</td>
</tr>
<tr>
<td>10E+10A</td>
<td><em>C. saucia</em></td>
<td>3.55±0.30</td>
<td>1.10±0.24</td>
<td>$Z = 4.51^*$</td>
</tr>
<tr>
<td>10E+5A</td>
<td></td>
<td>5.45±0.25</td>
<td>0.55±0.15</td>
<td>$Z = 5.51^*$</td>
</tr>
</tbody>
</table>

Data are Mean ±SE; *Significant at $P < 0.0001$.

Neonates of *C. transversalis* consumed more eggs than aphids in combinations of 10 eggs and 10 aphids (Wilcoxon test: $Z = 5.46; P < 0.0001; n = 20$) and 10 eggs and five aphids (Wilcoxon test: $Z = 5.16; P < 0.0001; n = 20$). The consumption difference was not significant at the low egg density (Wilcoxon test: $Z = 1.36; P > 0.05; n = 20$; Table I). MPI for *C. transversalis* at different combinations of prey densities revealed a preference for eggs rather than aphids (Table II).

Neonates of *C. saucia* consumed more eggs than aphids when presented in combinations of 10 eggs and 10 aphids (Wilcoxon test: $Z = 4.51; P < 0.0001; n = 20$) and 10 eggs and five aphids (Wilcoxon test: $Z = 5.51; P < 0.0001; n = 20$). The consumption difference was not significant at the low egg density (Wilcoxon test: $Z = 0.23; P > 0.1; n = 20$; Table I). MPI for *C. saucia* at different combinations of prey densities revealed a greater preference for eggs than aphids (Table II).

**Effect of egg-cannibalism on fitness components of developing neonates**

The developmental time, weight of newly emerged second instars, dry biomass of prey consumed during the first instar, and percent mortality of the three ladybird species, *P. dissecta*, *C. transversalis* and *C. saucia* fed eggs, mobile aphids and defenceless aphids are presented in Table III. The development of neonates of *P. dissecta* ($F = 71.99; P < 0.0001; df = 2, 59$), *C. transversalis* ($F = 104.42; P < 0.0001; df = 2, 72$) and *C. saucia*...
Table III. The effect of food (conspecific eggs, defenceless aphids and mobile aphids) on development time, weight of newly developed second instar and biomass consumption needed to reach second instar of three ladybird species.

<table>
<thead>
<tr>
<th>Ladybird species</th>
<th>Food</th>
<th>Development time (in days)</th>
<th>Weight (in mg)</th>
<th>Dry Biomass needed (in mg)</th>
<th>Mortality (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. dissecta</td>
<td>E</td>
<td>1.71 ± 0.38c</td>
<td>0.82 ± 0.10a</td>
<td>0.40 ± 0.05b</td>
<td>12.0%</td>
</tr>
<tr>
<td></td>
<td>DA</td>
<td>2.58 ± 0.07a</td>
<td>0.74 ± 0.10b</td>
<td>1.28 ± 0.17a</td>
<td>24.0%</td>
</tr>
<tr>
<td></td>
<td>MA</td>
<td>2.03 ± 0.08b</td>
<td>0.78 ± 0.15ab</td>
<td>1.22 ± 0.12a</td>
<td>16.0%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F = 71.99**</td>
<td>F = 2.66*</td>
<td>F = 338**</td>
<td>(\chi^2 = 5.21)</td>
</tr>
<tr>
<td>C. transversalis</td>
<td>E</td>
<td>0.92 ± 0.10c</td>
<td>0.81 ± 0.07a</td>
<td>0.50 ± 0.04b</td>
<td>0%</td>
</tr>
<tr>
<td></td>
<td>DA</td>
<td>1.56 ± 0.20a</td>
<td>0.49 ± 0.11c</td>
<td>1.43 ± 0.11a</td>
<td>0%</td>
</tr>
<tr>
<td></td>
<td>MA</td>
<td>1.19 ± 0.17b</td>
<td>0.70 ± 0.11b</td>
<td>1.50 ± 0.14a</td>
<td>0%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F = 104.42**</td>
<td>F = 71.79**</td>
<td>F = 679**</td>
<td>(\chi^2 = 4.34)</td>
</tr>
<tr>
<td>C. saucia</td>
<td>E</td>
<td>1.68 ± 0.34c</td>
<td>1.58 ± 0.55a</td>
<td>1.47 ± 0.19b</td>
<td>4.0%</td>
</tr>
<tr>
<td></td>
<td>DA</td>
<td>2.01 ± 0.26a</td>
<td>1.16 ± 0.43b</td>
<td>2.23 ± 0.23a</td>
<td>12.0%</td>
</tr>
<tr>
<td></td>
<td>MA</td>
<td>1.81 ± 0.34b</td>
<td>1.11 ± 0.27b</td>
<td>2.08 ± 0.10a</td>
<td>8.0%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F = 6.37*</td>
<td>F = 8.44**</td>
<td>F = 111.89**</td>
<td>(\chi^2 = 5.21)</td>
</tr>
</tbody>
</table>

E, eggs; DA, defenceless aphids; MA, mobile aphids. Data are Mean ± SE; *, ** Denote significant at \(P < 0.05\) and \(P < 0.001\), respectively. Means followed by the same letters within a column denote that the data are not statistically significant.

\(F = 6.37; P < 0.01; \text{df} = 2, 66\) was significantly faster when fed on conspecific eggs followed by mobile aphids and defenceless aphids.

The newly emerged second instar \(P. \text{dissecta} \ (F = 2.66; P < 0.05; \text{df} = 2, 59), C. \text{transversalis} \ (F = 71.79; P < 0.0001; \text{df} = 2, 72)\) and \(C. \text{saucia} \ (F = 8.44; P < 0.001; \text{df} = 2, 66)\) were heaviest after feeding on conspecific eggs compared to the other prey (Table III). The prey biomass consumed by the first instar \(P. \text{dissecta} \ (F = 338; P < 0.0001; \text{df} = 2, 59), C. \text{transversalis} \ (F = 679; P < 0.0001; \text{df} = 2, 72)\) and \(C. \text{saucia} \ (F = 111.89; P < 0.0001; \text{df} = 2, 66)\) was significantly lower when fed conspecific eggs compared to the other prey. No mortality occurred in neonates of \(C. \text{transversalis}\). However, mortality did occur for the other species with lesser mortality of neonates of \(P. \text{dissecta} \ (\chi^2 = 5.21; P < 0.05)\) and \(C. \text{saucia} \ (\chi^2 = 4.34; P < 0.05)\) when fed on conspecific eggs compared to the other prey (Table III).

Two-way ANOVA revealed significant effects of ‘species’ \(F = 214.62; P < 0.0001; \text{df} = 2, 214.62\), ‘food’ \(F = 96.46; P < 0.0001; \text{df} = 2, 201\), and the interaction between ‘species’ and ‘food’ \(F = 152.09; P < 0.0001; \text{df} = 4, 201\) on the developmental period. Significant effects of ‘species’ \(F = 101.15; P < 0.0001; \text{df} = 2, 214.62\), ‘food’ \(F = 21.54; P < 0.0001; \text{df} = 2, 201\), and the interaction between ‘species’ and ‘food’ \(F = 61.72; P < 0.0001; \text{df} = 4, 201\) on the weight of newly emerged second instars were also found. Two-way ANOVA revealed significant effects of ‘species’ \(F = 768.03; P < 0.0001; \text{df} = 2\) and ‘food’ \(F = 702.08; P < 0.0001; \text{df} = 2\), and the interaction between ‘species’ and ‘food’ \(F = 733.80; P < 0.0001; \text{df} = 4, 201\) on the dry prey biomass consumed by the first instars.

First prey contacted and eaten by neonates

The neonates of \(P. \text{dissecta}\) given choice between conspecific eggs and aphids, usually first contacted and consumed conspecific egg (Figure 1a,b). The mobility of aphids did not significantly affect rates of contact \(\chi^2 = 0.48; P > 0.1; \text{df} = 1\) and consumption \(\chi^2 = 3.58; P > 0.05\).
The first prey contacted and eaten by \textit{C. transversalis} and \textit{C. saucia} was not usually a conspecific egg. In \textit{C. transversalis}, the first prey contacted was affected significantly by mobility of aphids ($\chi^2 = 6.47$; $P < 0.05$; df = 1; Figure 1a,b). However, the first prey eaten was not significantly affected ($\chi^2 = 0.92$; $P > 0.1$; df = 1). In \textit{C. saucia}, the first meal contacted ($\chi^2 = 0.90$; $P > 0.1$; df = 1) and eaten ($\chi^2 = 0.75$; $P > 0.1$; df = 1) was not affected by mobility of aphids.

When compared between the species, the first prey contacted in presence of mobile ($\chi^2 = 12.32$; $P < 0.001$; df = 2) and defenceless aphids ($\chi^2 = 20.76$; $P < 0.001$; df = 2) varied significantly (Figure 1a,b). Similarly, the first prey eaten in the presence of mobile aphids ($\chi^2 = 41.76$; $P < 0.0001$; df = 2) and defenceless aphids ($\chi^2 = 18.00$; $P < 0.001$; df = 2) varied significantly (Figure 1a,b).

\textit{Chemical cues related to preferential cannibalism}

Neonates of \textit{P. dissecta} consumed significantly (Wilcoxon test: $Z = -4.17$; $P < 0.0001$; $n = 20$; Figure 2a) more aphids coated with egg extracts rather than eggs coated with aphid extracts. In the two control treatments, they consumed significantly more eggs.
coated with egg extract in presence of aphids (Wilcoxon test: $Z = 3.74; P < 0.0001; n=20$), and eggs in presence of aphids coated with aphid extract (Wilcoxon test: $Z = 3.89; P < 0.0001; n=20$).

Neonates of *C. transversalis* consumed more eggs coated with aphid extract than aphids coated with egg extract (Wilcoxon test: $Z = 2.53; P < 0.0001; n=20$; Figure 2b). In two control treatments, they consumed more eggs coated with egg extract in presence of aphids (Wilcoxon test: $Z = 2.84; P < 0.0001; n=20$), and eggs in presence of aphids coated with aphid extract (Wilcoxon test: $Z = 2.83; P < 0.0001; n=20$).

In two control treatments, neonates of *C. saucia* consumed significantly more eggs coated with egg extract in presence of aphids (Wilcoxon test: $Z = 4.51; P < 0.0001; n=20$; Figure 2c), and eggs in presence of aphids coated with aphid extract (Wilcoxon test: $Z = 5.51; P < 0.0001; n=20$). However, the consumption
difference was not significant when aphids coated with egg extracts and eggs coated with aphid extracts were provided (Wilcoxon test: $Z = 0.23; P < 0.0001; n = 20$).

**Discussion**

The neonates of *P. dissecta*, *C. transversalis* and *C. saucia* preferred conspecific eggs even in presence of suitable host aphids, *A. gossypii* and supports Gagne et al. (2002). However, the neonates of the three ladybird species responded differently at lower egg density with only *P. dissecta* maintaining its preference for conspecific eggs. This behaviour might be attributed to the size of predator, efficiency of prey consumption, and degree of satiation. Neonates of *C. transversalis* and *C. saucia* are larger than *P. dissecta* (in terms of length and weight; Omkar unpublished data), and it seems likely that they would have a greater predation potential and gut capacity. Hence, more prey biomass may be needed for their survival and development.

Conspecific eggs were more nutritious to neonates of the three ladybird species when compared to mobile aphids and defenceless aphids. Neonates that fed on conspecific eggs developed faster and were heavier than those fed on aphids. In addition, they consumed less dry biomass of conspecific eggs than aphids during the instar. The evidence from a metabolic pool model (Baumgartner et al. 1987) reveals that bioconversion efficiency for conspecific eggs is greater than that for aphids. The higher nutritional value of conspecific eggs could be due to high cholesterol content in conspecific eggs (MacDonald et al. 1990).

There was a significant effect of ‘species’ and ‘food’ of the neonates on their developmental time, weight and dry prey-biomass needed for the development. In all these parameters, conspecific eggs were better food followed by mobile and defenceless aphids. There was a significant interaction between ‘species’ and ‘food’.

Neonates of *P. dissecta* preferentially attacked and ate conspecific eggs when provided a choice with mobile or defenceless aphids. This reveals that prey vulnerability was not the factor responsible for egg–cannibalism by the neonates. It also reveals discrimination of the more nutritious food by the neonates of *P. dissecta*. Our findings support Gagne et al. (2002), who suggested that neonates select for nutritionally richer foods and that egg–cannibalism does not result from frequency of encounters and immobility of eggs. These results suggest that the chemical nature of the cuticular waxes, rather than frequency of encounter, is more important to prey discovery (Agarwala & Dixon 1992). Food discrimination was, however, not found in the neonates of *C. transversalis* and *C. saucia* possibly due to their bigger size and greater energy requirement.

Chemical cues play an important role mating, prey detection (Hemptinne et al. 2000, 2001; Omkar et al. 2004) and mate search (Hemptinne et al. 1998; Omkar & Pervez 2005) in ladybirds. The chemicals, probably certain alkanes (Hemptinne et al. 2001) on the egg surfaces, provide a cue to the neonates for prey location (about their first meal). In present investigation, neonates of *P. dissecta* responded to the extracts of the eggs by cannibalising the eggs. After interchanging a surface coating of crushed prey, i.e., conspecific eggs were coated with aphid-extract and aphids with egg-extract, the behavioural response of neonates was reversed. This reveals that they were more responsive to the extracts of conspecific eggs. The effect of chemical cues, however, was not found in the other two ladybird species, even though they ate significantly more conspecific eggs than aphids.
The series of experiments has provided results relevant to the questions raised in the past, notably 'why do ladybirds lay eggs in cluster?' (Agarwala & Dixon 1993) and 'why do females lay trophic eggs mixed with viable eggs?' (Dixon 2000). The present investigation is relevant indirectly by revealing preference for conspecific eggs by neonates. The egg-clustering possibly eases the neonates search to find their first meal. The female ladybird lays trophic or nurse eggs within the clusters, which are nonviable and deemed for consumption by the neonates (Dixon 2000). No information is available on the prey-dependent bio-kinetics (in terms of energy consumption by walking and searching) of the ladybird larvae. To understand better the female strategy of laying trophic eggs, studies are needed to find out the effect of first meal on speed of walking and searching of neonates.

Thus, it can be concluded that: neonates of *P. dissecta*, *C. transversalis* and *C. saucia* prefer to eat conspecific eggs in presence of their essential prey, the aphid, *A. gossypii*. This preference was stronger in *P. dissecta* than the other two species. Neonates of all the three species developed faster and heavier with least mortality when fed on conspecific eggs as compared to mobile or defenceless aphids. Lesser dry biomass of eggs compared to that of aphids was consumed by first instars. Neonates of *P. dissecta* contacted and ate conspecific eggs more frequently than aphids when given a choice for their first meal. Finally, chemicals present on surface and within eggs appear to be involved in attracting the neonates of *P. dissecta* for egg–cannibalism.

Acknowledgements
Authors thank Dr Robert L. Koch, Department of Entomology, University of Minnesota, Minnesota, USA and two anonymous reviewers for critically reading the previous drafts of the manuscript and providing suggestions. AP is thankful to Council of Scientific and Industrial Research, New Delhi for financial assistance in the form of Research Associateship.

References
Egg–cannibalism in presence of aphids by ladybirds


