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Larval cannibalism in aphidophagous ladybirds: Influencing factors, benefits and costs

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Abstract

The influence of food availability, food quality, size disparity and density on larval cannibalism in two aphidophagous ladybirds, *Propylea dissecta* and *Coccinella transversalis*, was studied in the laboratory. Both species were cannibalistic; however, the rate of cannibalism was greater in the former species. Cannibalism increased with reduced food availability rather than reduced food quality. Size disparity increased larval cannibalism in both species. Cannibalism rate also increased with an increase in larval density. The high rate of cannibalism by first instars was recorded at high larval density. Larvae fed conspecific eggs throughout the development were heavier than those fed conspecific larvae, but weighed less than larvae fed aphids, *Aphis gossypii*. Larval cannibalism was not advantageous in terms of development and body weight. However, egg cannibalism by first instars was advantageous resulting in fast development and heavier second instars.

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1. Introduction

Cannibalism, a perfectly natural behaviour for many species of insects and mites (Elgar and Crespi, 1992), is a common occurrence in predaceous ladybirds (Coleoptera: Coccinellidae) and confers nutritional and competitive advantages to the cannibals (Gagne et al., 2002; Osawa, 2002; Snyder et al., 2000). This behaviour may evolve if the evolutionary costs are less than the benefits. The likely costs of cannibalism are: (i) risk of injury (Dawkins, 1976), (ii) reduction in inclusive fitness if relatives are attacked (Hamilton, 1964a,b) and (iii) risk of disease transmission (Hurst and Majerus, 1993; Majerus and Hurst, 1997). Larval cannibalism represents a survival strategy of the larvae under prey scarce conditions (Dixon, 2000; Kindlmann and Dixon, 1993; Yasuda and Shinya, 1997). This enables the fittest survivors to thrive on conspecifics and complete their

development. On becoming adults, they are then able to fly to other prey sites for reproduction and subsistence.

Cannibalism of eggs, lower and same stage larvae, prepupae and pupae by ladybird larvae is frequent in the laboratory as well as the fields (Dixon, 2000). Larval cannibalism is a function of relative vulnerability and frequency of encounters (Agarwala and Dixon, 1993). However, a recent study on different components of cannibalism on three ladybird species, viz. *Harmonia axyridis* (Pallas), *Cycloneda sanguinea* Linnaeus and *Olla v-nigrum* (Mulsant) revealed that it is largely dependent on the species, food availability, degree of relatedness, size disparity and larval density (Michaud, 2003). These ladybird larvae also complete development feeding on conspecific eggs or larvae (Michaud, 2003). Third instars of *H. axyridis* avoid eating younger relative larvae (Joseph et al., 1999). This was made possible by kin recognition, which was seemingly enabled by endogenous cues.

Propylea dissecta (Mulsant) and *Coccinella transversalis* Fabricius are two aphidophagous ladybirds of the oriental

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region, which co-occur and preferentially feed on the aphid *Aphis gossypii* Glover (Omkar and James, 2004; Pervez and Omkar, 2004). Larvae of both species are better cannibals than intraguild predators, preferring to eat conspecific than heterospecific eggs (Omkar et al., 2004, 2005a). We attempt to replicate the experimental approach of Michaud (2003) using *P. dissecta* and *C. transversalis*. Instead of *Ephestia* eggs provided as food by Michaud (2003), we used natural food (*A. gossypii*) to determine the effects of food availability and food quality, size disparity and population density on larval cannibalism. Larvae were also reared exclusively on diets of conspecifics eggs and larvae to assess the developmental consequences of cannibalism in comparison to a diet of *A. gossypii*.

2. Materials and methods

2.1. Stock colony maintenance

Adults *P. dissecta* and *C. transversalis* were collected from the fields of bottle gourd (*Lagenaria vulgaris* Seringe), where they were preying on *A. gossypii* and brought to the laboratory to form stock cultures. Pairs of each ladybird species were kept in Petri dishes (9.0×2.0 cm) and fed daily on ad libitum supply of *A. gossypii* on pieces of *L. vulgaris* leaves (27 ± 1 °C temperature, $65 \pm 5\%$ RH and 12:12 LD photoperiod). Eggs were collected daily and first instar larvae were used in all experiments. All experiments were performed in Petri dishes (size as above) with third instar *A. gossypii* as prey.

2.2. Comparative larval cannibalism in two ladybird species

Neonates of *P. dissecta* and *C. transversalis* were reared in groups consisting of three conspecifics per Petri dish (9.0×2.0 cm) with a daily supply of 20 *A. gossypii*. Each Petri dish was examined daily to record mortality, cannibalism, moulting and pupation. The experiment was replicated 20 times. The number of replicates with one or two cannibalism events were recorded. Data on cannibalism events were analyzed by χ^2 test (Minitab, 2000).

2.3. Effect of food availability and food quality on cannibalism

Neonates of *P. dissecta* and *C. transversalis* were reared in groups consisting of three conspecifics per Petri dish. Three treatments of food were made: (i) ad libitum *A. gossypii*, as a control, (ii) 20 *A. gossypii* daily as a limited high-quality food and (iii) ad libitum supply of *Aphis nerii* Boy. as poor quality food (Omkar and James, 2004; Omkar and Mishra, 2005). Cannibalism trials included 20 replicates to determine whether cannibalism varies as a function of food availability or food quality. All replicates were examined daily for mortality, cannibalism, molting and pupation. The data were square root transformed and subjected to three-way ANOVA with species, time and treatment as independent variables (SAS, 2002).

2.4. Effect of size disparity on larval cannibalism

The effect of degree of size disparity among larvae on rates of cannibalism was determined by grouping conspecific larvae of *P. dissecta* and *C. transversalis* with variation in size and instar. Three treatments were used: (i) 3 second instars, (ii) 1 third and 2 first instars and (iii) 1 fourth and 2 first instars, each with 10 aphids. The experiment was replicated 20 times. Each replicate was examined daily for mortality, cannibalism, moulting and pupation. The rates of single and double cannibalism events was compared among treatments by χ^2 test (Minitab, 2000). The number of replicates with one or more cannibalism events were compared. The data on cannibalism were square root transformed and subjected to two-way ANOVA with species and treatment as independent variables (SAS, 2002).

2.5. Effect of larval density on cannibalism

The effect of larval density on cannibalism was studied using different densities of conspecific first instars of *P. dissecta* and *C. transversalis* in a Petri dish (size as above) containing 40 individuals of *A. gossypii*. Neonates of each species taken from the egg clusters of different females were kept together in a group of two, four and eight per Petri dish. Daily observations were made and prey were replenished daily. The experiment was replicated 20 times and all replicates were examined daily to record mortality, cannibalism, moulting and pupation. The number of larvae were corrected and the incidence of cannibalism was compared by χ^2 test (Minitab, 2000).

2.6. Development, weight and mortality of larvae fed on conspecific eggs and larvae

To determine the effect of conspecific eggs and larvae as food on the development, weight and mortality of four larval instars, three treatments were made. First instars of each ladybird species were reared singly on ad libitum supply of (i) conspecific eggs, (ii) conspecific first instars and (iii) *A. gossypii*. In the second treatment, 1-day-old first instars, reared on *A. gossypii*, were used as cannibal and conspecific neonates. Observations on the molts of larvae were taken thrice a day and developmental period (from hatching of egg to adult emergence), weight (weighed 3 h after each moult) and mortality recorded. The experiment was replicated 10 times ($n = 10$). The mortality of larvae fed on different diets were compared using χ^2 test (SAS, 2002). The weight of larval instars of each ladybird species was subjected to one-way ANOVA (SAS, 2002). The means were compared with post hoc Tukey's honest test of significance at 95% confidence level. The data on larval developmental period, and weight of each instar were subjected to two-way ANOVA with species (two levels) and food (three levels) as independent variables (SAS, 2002).

3. Results

3.1. Comparative larval cannibalism in two ladybird species

The results revealed occurrence of one or more events of cannibalism in both ladybird species, viz. *P. dissecta* and *C. transversalis* (Table 1). The incidence of both single ($\chi^2 = 33.33$; $P < 0.0001$; df = 1) and double ($\chi^2 = 10.67$; $P < 0.001$; df = 1) cannibalism events was significantly higher in *P. dissecta* than in *C. transversalis*.

3.2. Effect of food availability and food quality on cannibalism

Cannibalism events varied as a function of reduced food availability but not reduced food quality, as the number of events was significantly increased for reduced food availability in both ladybird species (Figs. 1a and b). The differences in the events of cannibalism were significant between reduced food availability and food quality from days 3 to 7 in *P. dissecta*, and from days 3 to 9 in *C. transversalis* (Figs. 1a and b). Double cannibalism events were recorded in the reduced prey availability by both ladybird species. Three-way ANOVA revealed a significant main effect of time ($F = 77.19$; $P < 0.0001$; df = 8) and treatment ($F = 269.06$; $P < 0.0001$; df = 2). The main effect of species ($F = 0.36$; $P > 0.1$; df = 1) was not significant. The interaction between species, time and treatment was also significant ($F = 106.73$; $P < 0.0001$; df = 11, 948).

3.3. Effect of size disparity on larval cannibalism

The incidence of cannibalism among *P. dissecta* larvae increased with an increase in size disparity (Fig. 2) and the frequency of both single ($\chi^2 = 10.75$; $P < 0.01$; df = 2) and double ($\chi^2 = 15.51$; $P < 0.01$; df = 2) cannibalism events was affected. In *C. transversalis*, the incidence of cannibalism by third and fourth instars were similar and higher than that of second instars. The differences in frequency of a single cannibalism event between the treatments in *C. transversalis* was statistically significant ($\chi^2 = 10.75$; $P < 0.01$; df = 2). Double cannibalism events did not occur in *C. transversalis*. There was a significant ($F = 26.94$; $P < 0.0001$; df = 2) main effect of treatment on the events of cannibalism as a function of size disparity. The interaction between species and teatment was also significant ($F = 18.20$; $P < 0.0001$; df = 13, 116). The main
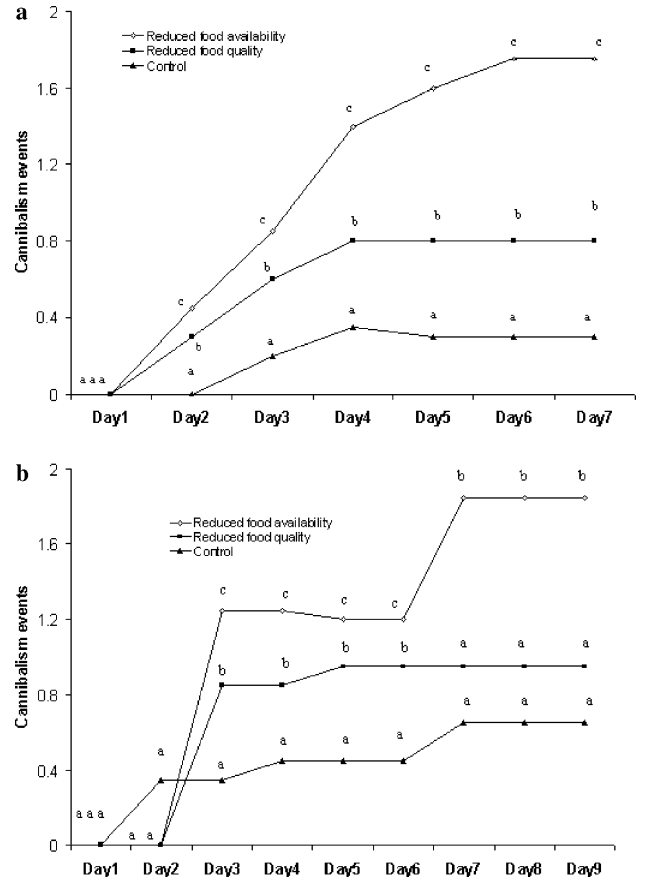

Fig. 1. (a) Cumulative number of cannibalism events per replicate in *P. dissecta* larvae when receiving three different treatments: (i) reduced food availability, (ii) reduced food quality, and (iii) food availability (control). Different letters between the treatments indicate that data are statistically significant. (b) Cumulative number of cannibalism events per replicate in *C. transversalis* larvae when receiving three different treatments: (i) reduced food availability, (ii) reduced food quality, and (iii) food availability (control). Different letters between the treatments indicate that data are statistically significant.

effect of species was, however, not significant ($F = 0.73$; $P > 0.1$; df = 1).

3.4. Effect of larval density on cannibalism

The incidence of cannibalism increased with an increase in larval density in both *P. dissecta* ($\chi^2 = 13.79$; $P < 0.0001$; df = 2) and *C. transversalis* ($\chi^2 = 43.24$; $P < 0.0001$; df = 2). Comparison of data between species was also significant ($\chi^2 = 61.08$; $P < 0.0001$; df = 5). Cannibalism in the high density treatment was higher for first instars than for other conspecific instars in *P. dissecta* (Fig. 3). Cannibalism in the high density treatment for third instars of *C. transversalis* was higher than other conspecific instars (Fig. 3).

3.5. Development, weight and mortality of larvae fed on conspecific eggs and larvae

A significant effect of the different foods was recorded on the developmental period and weights of four larval instars

Table 1
Relative incidence of cannibalism among larvae of *P. dissecta* and *C. transversalis* raised from first instars in groups of three

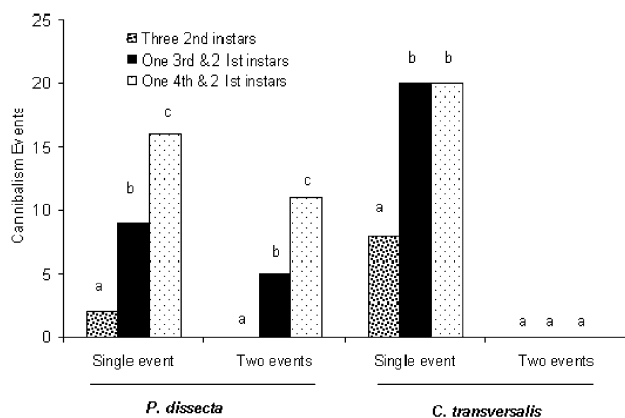| Species	n	Percentage of replicates with one event	Percentage of replicates with two events
P. dissecta	20	80	35
C. transversalis	20	40	15
χ^2 test		$\chi^2 = 33.33$; $P < 0.0001$	$\chi^2 = 10.67$; $P < 0.001$

Fig. 2. Total number of cannibalism events among larvae of *P. dissecta* and *C. transversalis* in three different treatments representing different levels of size disparity. Different letters within the treatment indicate that data are statistically significant.
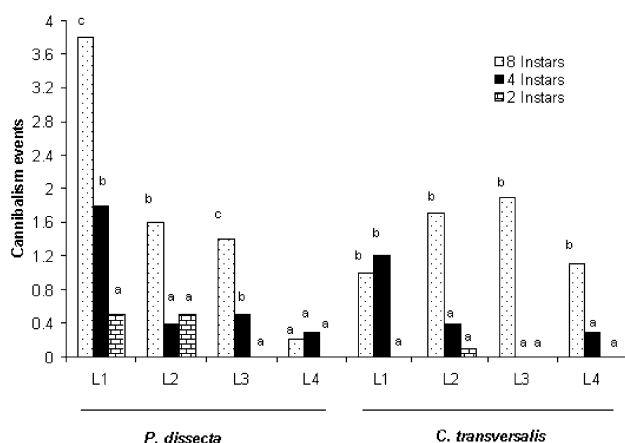

Fig. 3. Total number of cannibalism events by different instar larvae of *P. dissecta* and *C. transversalis* in three treatments representing different levels of larval density. Different letters within the treatment indicate that data are statistically significant.

of *P. dissecta* and *C. transversalis* (Tables 2 and 3). Larvae of both ladybird species developed when fed exclusively on conspecific eggs and larvae. Mortality of *P. dissecta* larvae

was 0, 10 and 20% ($\chi^2 = 22.22$; $P < 0.001$) and that of *C. transversalis* larvae was 0, 10 and 30% ($\chi^2 = 40.39$; $P < 0.001$) when fed on aphid, conspecific eggs and conspecific larvae, respectively. Development was faster and larvae heavier when fed on aphids, followed by conspecific eggs, followed by larvae (Tables 2 and 3).

Two-way ANOVA revealed a significant main effect of species ($F = 17.34$; $P < 0.0001$; df = 1) and food ($F = 15.57$; $P < 0.0001$; df = 2) on the development of first instars and the interaction between species and food was also significant ($F = 16.16$; $P < 0.0001$; df = 3, 56). The duration of the second instar was significantly affected by both species ($F = 5.91$; $P < 0.05$; df = 1) and food ($F = 27.61$; $P < 0.0001$; df = 2) and the interaction between species and food was also significant ($F = 20.40$; $P < 0.0001$; df = 3, 56). The duration of the third instar was significantly affected by both species ($F = 27.01$; $P < 0.0001$; df = 1) and food ($F = 28.52$; $P < 0.0001$; df = 2) and also resulted in a significant interaction ($F = 28.08$; $P < 0.0001$; df = 3, 56). The duration of the fourth instar was significantly affected by species ($F = 22.06$; $P < 0.0001$; df = 1) and food ($F = 46.08$; $P < 0.0001$; df = 2) levels and resulted in a significant interaction ($F = 38.07$; $P < 0.0001$; df = 3, 56).

A significant main effect of species ($F = 36.79$; $P < 0.0001$; df = 1) and food ($F = 40.17$; $P < 0.0001$; df = 2) was found on the weight of first instars and the interaction between species and food was also significant ($F = 39.04$; $P < 0.0001$; df = 3, 56). The weight of second instars was significantly affected by both species ($F = 40.10$; $P < 0.0001$; df = 1) and food ($F = 57.48$; $P < 0.0001$; df = 2) levels. The interaction between the two independent variables was significant ($F = 51.68$; $P < 0.0001$; df = 3, 56). A significant main effect of species ($F = 82.06$; $P < 0.0001$; df = 1) and food ($F = 58.76$; $P < 0.0001$; df = 2) was also recorded on the weight of third instar and resulted in a significant interaction ($F = 66.53$; $P < 0.0001$; df = 3, 56). The weight of fourth instar was also significantly affected by both species ($F = 144.04$; $P < 0.0001$; df = 1) and food ($F = 166.88$; $P < 0.0001$; df = 2). The interaction between these two independent variables was also significant ($F = 159.27$; $P < 0.0001$; df = 3, 56).

Table 2
Development duration (in days) of larval instars of *P. dissecta* and *C. transversalis* when reared on conspecific eggs, conspecific larvae or *A. gossypii* (control)

Ladybird species	Larval instars	Food			F value[*]
		Conspecific eggs	Conspecific larvae	Aphid (*A. gossypii*)	
P. dissecta	L_1	1.60 ± 0.21b	1.99 ± 0.15a	1.65 ± 0.21b	11.92
	L_2	1.67 ± 0.17b	2.29 ± 0.27a	1.76 ± 0.20b	23.46
	L_3	1.49 ± 0.13b	2.13 ± 0.27a	1.38 ± 0.20b	38.89
	L_4	2.41 ± 0.19b	2.92 ± 0.11a	2.15 ± 0.10c	81.23
C. transversalis	L_1	2.05 ± 0.014a	2.14 ± 0.16a	1.73 ± 0.29b	10.60
	L_2	2.36 ± 0.25a	2.43 ± 0.30a	1.51 ± 0.22b	38.68
	L_3	2.02 ± 0.16a	2.10 ± 0.21a	1.79 ± 0.16b	8.03
	L_4	2.52 ± 0.34b	3.08 ± 0.16a	2.67 ± 0.20b	14.25

L_1, L_2, L_3 and L_4 denote for first, second, third and fourth instars, respectively. Values are mean ± SD. Different letters between the columns denote that means are statistically significant.
[*] Significant at $P < 0.001$; Tukey's test range = 3.51; df = 2, 27.

Table 3
Weight (in mg) of larval instars of *P. dissecta* and *C. transversalis* reared on conspecific eggs, conspecific larvae and *A. gossypii* (control)

Ladybird species	Larval instars	Food			*F* value[*]
		Conspecific eggs	Conspecific larvae	Aphid (*A. gossypii*)	
P. dissecta	L$_1$	0.83 ± 0.09a	0.39 ± 0.09c	0.71 ± 0.12b	50.06
	L$_2$	2.71 ± 0.63a	1.81 ± 0.16b	3.06 ± 0.23[a]	25.86
	L$_3$	4.42 ± 0.93b	4.55 ± 0.60b	6.03 ± 0.47a	16.59
	L$_4$	8.79 ± 0.79b	8.39 ± 0.38b	13.24 ± 0.70a	174.37
C. transversalis	L$_1$	0.84 ± 0.10a	0.55 ± 0.05b	2.12 ± 0.06c	1299
	L$_2$	2.67 ± 0.41a	2.62 ± 0.17a	5.07 ± 0.37b	174.27
	L$_3$	6.28 ± 1.07b	5.37 ± 0.21a	9.03 ± 0.38c	85.42
	L$_4$	12.57 ± 0.22b	10.49 ± 1.96a	16.69 ± 0.51c	72.15

L$_1$, L$_2$, L$_3$ and L$_4$ denote first, second, third and fourth instars, respectively. Values are mean ± SD. Different letters denote that means are statistically significant.

  [*] Significant at $P < 0.0001$; Tukey's test range = 3.51; df = 2, 27.

4. Discussion

The results revealed that both *P. dissecta* and *C. transversalis* engaged in larval cannibalism, however, it was more frequent in the former species. There were greater incidences of egg-cannibalism by the neonates of *P. dissecta* than *C. transversalis* (Omkar et al., 2004, 2006a). This collectively indicates that cannibalistic trait is stronger in the former species. *Propylea dissecta* (Omkar and Mishra, 2005; Omkar and Pervez, 2004) has a higher net reproductive rate (R_o) and intrinsic rate of increase (r_m) than *C. transversalis* (Omkar et al., 2005b). This suggests that due to increased reproduction and high survival of *P. dissecta*, there might be an intraspecific competition for food and space. Higher rates of cannibalism by *P. dissecta* than those of *C. transversalis* could be a possible reason for the autoregulation of its population. Similarly, Michaud (2003) found that the intrinsic rate of larval cannibalism in *C. sanguinea* was significantly higher than that in *O. v-nigrum* and *H. axyridis*. Our results show that the incidence of larval cannibalism was greatly increased under conditions of reduced food availability, more so than under conditions of food quality. This finding is similar to that of Michaud (2003), where the rate of cannibalism in *H. axyridis*, *O. v-nigrum* and *C. sanguinea* significantly increased with reduction in the quantity of food supplied. Food shortages experienced by *Delphastus pussillus* LeConte larvae of different ages also resulted in increased rate of cannibalism (Gerling and Stern, 1993). The egg and larval cannibalism by *Adalia bipunctata* Linnaeus was inversely proportionate to food availability (Agarwala and Dixon, 1992). Schellhorn and Andow (1999) observed high rates of cannibalism in three co-occurring ladybirds when aphid populations crashed.

The main effect of treatment, i.e. size disparity, was significant on the events of cannibalism. This indicates that larval cannibalism was a function of size disparity and incidence of cannibalism increased with an increase in size disparity between cannibal and victim. This was because an attacker has significantly reduced risk associated with attacking a smaller conspecific than the one of same size. The relative inferiority of victim larvae in terms of body size, weight and walking speed is also a reason for this increased cannibalism (Agarwala et al., 2003; Omkar et al., 2006b). The first instars of *Coccinella septempunctata brucki* Mulsant were more frequently attacked and cannibalized by older instars (Takahashi, 1987). Younger instars of *A. bipunctata* were also most vulnerable to cannibalism by older ones (Agarwala and Dixon, 1992). The main effect of species on the events of cannibalism was not significant suggesting that size disparity between cannibal and victim generally increases the probability of cannibalism among ladybird larvae.

In the present study, the incidence of cannibalism increased with the increase in larval density, which reveals a density-dependent effect. This might be due to the increased rate of encounter between cannibals and victims. The present study conforms the finding of Dimetry (1976) who concluded that larval overcrowding, increased the rate of cannibalism among all instars of *A. bipunctata*. The incidence of larval cannibalism in *H. axyridis* at higher larval density was 50% more than at lower density (McClure, 1987). Our results support the inferences of Kindlmann and Dixon (1993), who suggested that incidence of cannibalism increases in declining aphid colonies because of increase in predator density.

Larvae of both ladybird species managed to complete their development after being reared on exclusive diets of either conspecific eggs or larvae. Food is an important component and strongly affects the biology of ladybirds (Hodek and Honek, 1996). A significant effect of diet on the weights of various larval instars was observed. Though larvae reared on conspecific eggs were heavier than those reared on conspecific larvae, they were still lighter than those fed on *A. gossypii*. This suggests that egg cannibalism could provide an initial advantage to the cannibal by providing immediate nutritional requirements to complete development, to get them their first meal or to eliminate the potential competitors.

Eating conspecific eggs and larvae also resulted in few mortality and delayed development. Cannibalism could be advantageous to a ladybirds if it becomes cannibal at some point in its development and can then switch back to

normal predatory habits (Omkar et al., 2004; Snyder et al., 2000).

First instars of *P. dissecta* weighed more after feeding on conspecific eggs than on aphids, suggesting that conspecific eggs could be most nutritious to first instars. Gagne et al. (2002) reported that neonates of an aphidophagous ladybird, *Coleomegilla maculata lengi* Timberlake preferentially eat conspecific eggs even in presence of aphids, as the former was more nutritious. This was further supported in a ladybird, *Coelophora biplagiata* (Swartz) (Omkar et al., 2006a). By the time first instars of *P. dissecta* larvae fed on conspecific eggs reached the fourth instar, they were significantly lighter than those reared on aphids, suggesting that egg cannibalism could be especially advantageous to a specific life stage. The larvae of *H. axyridis*, *C. septempunctata brucki* and *A. bipunctata* also completed their development on conspecific eggs but failed to do so when provided with heterospecific eggs (Sato and Dixon, 2004).

Michaud (2003) found high costs of larval cannibalism in terms of decreased survival, prolonged development time, and reduced weight in larvae of *C. sanguinea* and *O. v-nigrum* when these were reared on exclusive diet of conspecific larvae. Finding no measurable benefits he concluded that an exclusive diet of conspecific larvae for the entire development period was not a realistic possibility in nature, but the conspecific eggs represented better nutrition than conspecific larvae as function of being less developed and therefore easier to digest. Our results support his finding, as the benefits of egg cannibalism evident from first instars were clearly absent in the case of larval cannibalism. It is likely that larval cannibalism can provide individual benefits in terms of reduced intraspecific competition and survival benefits if prey are scarce, then conspecific larvae can be used as a temporary food to bridge the gap in prey availability. The costs of larval cannibalism are much higher than egg cannibalism because of the increased risk of injury, eggs on the other hands defenseless.

It can be concluded that: (i) rate of larval cannibalism is intrinsically higher in *P. dissecta* than in *C. transversalis*, (ii) larval cannibalism is more dependent on food availability than food quality, (iii) incidence of larval cannibalism increases with increase in size disparity between cannibal and victim, (iv) larval cannibalism is density-dependent and increase with increasing population density and (v) larvae of both ladybird species can be reared on exclusive egg and larval diets, however an egg diet is more suitable.

Acknowledgments

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