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Attack, escape and predation rates of larvae of two aphidophagous ladybirds during conspecific and heterospecific interactions

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Abstract

The attack, escape and predation rates for larvae of aphidophagous ladybird *Propylea dissecta* (Mulsant) and *Coccinella transversalis* Fabricius were quantified as a potential mechanism leading to the differences in the incidence of cannibalism and intraguild predation. These rates were compared at four larval instars within and between the species. The attack rates of larvae of *C. transversalis* were significantly higher than those of *P. dissecta* towards conspecific and heterospecific victims. For both species, third instars exhibited maximum tendency to attack. Escape rates in *C. transversalis* were higher than *P. dissecta*. In *P. dissecta*, the second instars made a greater number of escapes than other conspecific instars after being attacked by same stage cannibal or heterospecific predator. In *P. dissecta*, first instars suffered maximum mortality due to cannibalism and intraguild predation by conspecifics and heterospecifics of the same and older developmental stage. No larvae of *C. transversalis* were eaten by *P. dissecta* of the same stage. These results suggest that the larvae of *P. dissecta* were more often potential cannibals than intraguild predators, while the reverse was the case in *C. transversalis*. Based on this finding, it could be predicted that in patchy prey habitats, high rates of larval cannibalism in *P. dissecta* would occur with a high risk of cannibalism of first instars. Larvae of *C. transversalis* would respond as intraguild predators, while those of *P. dissecta* as intraguild prey. The greater size and walking activity of *C. transversalis* could be possible reason for this tendency.

Keywords: *Coccinella transversalis*, *Propylea dissecta*, *cannibalism*, *intraguild predation*, *Coccinellidae*, *aphids*, *Aphis gossypii*

Introduction

In biological communities, complex interactions and more specifically cannibalism and intraguild predation (IGP), are considered to be important determinants of population dynamics and community structure (Polis et al. 1989; Polis & Holt 1992; Omkar et al. 2002). These interactions within and between niche-partitioning predators have been drawing much scientific attention and are highly prevalent in guilds of insect predators, especially in ladybirds (Agarwala & Dixon 1991; Rosenheim et al. 1995; Yasuda & Shinya 1997; Yasuda & Ohnuma 1999; Yasuda

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et al. 2001; Burgio et al. 2002; Agarwala et al. 2003). Cannibalism and IGP decide the fate of a community (e.g., stabilized predator–prey dynamics) (Godfray & Pacala 1992). These interactions are advantageous to the species, as they reduce competition and protect depleting food resource, provide immediate nutritional gain, and thereby protect the gene pool (Dixon 2000; Snyder et al. 2000). The possible costs associated with these interactions among predators are that the predator could become the victim (Elgar & Crespi 1992), there is a loss of inclusive fitness (Agarwala & Dixon 1993; Joseph et al. 1999), risk of injury, toxicity or disease transmission (Pfenning 1997; Hurst & Majerus 1993), and delayed development and dwarfism in emerging adults (Michaud 2003).

Little is known about the integral components of these interactions, i.e., attack, escape and predation rates, which are directly associated with cannibalism and IGP in ladybirds (Yasuda et al. 2001). *Harmonia axyridis* (Pallas) exhibited higher attack and predation rates than *Coccinella septempunctata* Linnaeus in the laboratory, which may explain the displacement of the latter species and other ladybird species by the former in several places in the world (Yasuda et al. 2001; Koch 2003). Similar competitive interactions between *C. septempunctata* and *Coleomegilla maculata* (de Geer) revealed the former to be dominant; however, due to temporal and spatial differences in their feeding habits, the former is not an intraguild predator of the latter (Obrycki et al. 1998).

Propylea dissecta (Mulsant) and *Coccinella transversalis* Fabricius are aphidophagous ladybirds of the Oriental region, coexisting in local agricultural fields sharing common prey resources. Individuals of *P. dissecta* have a limited prey range with high tolerance against stresses, like prey deprivation and extreme temperatures (Omkar & Pervez 2003, 2004; Pervez & Omkar; 2004a,b). In contrast, *C. transversalis* has a wider prey range (Evans 2000; Omkar & Pervez 2004). Interactions of *C. transversalis* with its prey (James 2001; Omkar & James 2004) and other aphidophaga (Agarwala et al. 1998, 2003) have been studied but little information on its interaction with *P. dissecta* (Omkar et al. 2004). The potential for intraguild interactions among these species seems less likely because of their stable coexistence in habitats, where prey are abundant. This was supported by the evidence indicating that their larvae and adults have a tendency to attack conspecific more than heterospecific eggs (Omkar et al. 2004). Thus, it would be interesting to determine their status in an intraguild combat where aphid prey is a limiting factor.

Thus, the present study was designed to investigate the components of larval cannibalism and IGP in the form of attack, escape and predation rates of *P. dissecta* and *C. transversalis*. We aimed to (i) examine inter and intraspecific behavioral events and to predict the fate of interactions in the field in prey absence, (ii) evaluate the relative tendency of cannibalism in two species in prey absence, and (iii) determine the status of *P. dissecta* and *C. transversalis* in terms of intraguild predator and intraguild prey.

Materials and methods

Stock maintenance

Adults of *P. dissecta* and *C. transversalis* were collected from fields of bottle gourd, *Lagenaria vulgaris* Seringe, preying on *A. gossypii*, and brought to the laboratory to maintain stock culture. For stock, pairs of each species were kept in Petri dishes (9.0 × 2.0 cm) to allow mating and were fed daily an *ad libitum* supply of *A. gossypii* on pieces

of *L. vulgaris* leaves ($27 \pm 1^\circ\text{C}$ temperature, $65 \pm 5\%$ R.H. and 12:12 LD photo-period). Eggs laid were collected daily. The hatched first instars were reared on *A. gossypii* to desired larval stages (L_1 , L_2 , L_3 and L_4) to be used in experiments performed in Petri dishes.

Body length, body weight and walking activity of larvae

The body length, body weight and walking activity (in terms of distance travelled in 1 min) of all the four instars of *P. dissecta* and *C. transversalis* were measured. The body length was measured by placing the larva on a point on graph paper, holding it firmly but gently and allowing it to extend naturally; the distance between the tip of the head and the abdomen was measured in 10 replicates ($n = 10$). The larva was then weighed (0.1 mg precision) using an electronic balance (SARTORIUS-H51) ($n = 10$). To determine walking activity, a 12-h starved larva was placed on a 100-cm long glass rod and allowed to walk. The distance travelled by the larva in 1 min was recorded ($n = 10$). Data on body length, body weight and walking activity of larvae were subjected to one-way ANOVA followed by Tukey's test of significance (SAS 2002).

Attack, escape and predation rates of larvae

All four instars of *P. dissecta* and *C. transversalis* were isolated in separate Petri dishes (size as above) and starved for 12 h to induce similar levels of hunger. Two sets of inter and intraspecific predation studies were made.

In the first set of studies, larvae of the same stage were kept in Petri dishes, i.e., L_1 with L_1 , L_2 with L_2 , L_3 with L_3 , and L_4 with L_4 . Thus, four intraspecific combinations were created and four intraspecific combinations of each species were created. This collectively resulted in 12 combinations of same stage larval interactions.

In the second set of studies, a larva was paired with another larva of one instar older than itself resulting in the following combinations: L_1 with L_2 , L_2 with L_3 , and L_3 with L_4 . Thus, six combinations of intraspecific and interspecific predation were made.

The two larvae were placed in a Petri dish (size as above) without food. Continuous observations were made for 1 h on the sequence of behaviors between larvae, i.e., contacts, attacks, escapes and predation events in 20 replicates.

From the possible sequence of behaviors between two larvae, attack rate (number of individual attacked/ number of individual contacted), escape rate (number of individual escaped/number of individual attacked) and predation rate = (number of individual eaten/20) were calculated. The data on the attack, escape and predation rates were subjected to arcsine square root transformation and analyzed using one-way ANOVA. This was followed by a post hoc test, i.e., Fisher's protected least significant differences (PLSD) (SAS 2002).

Results

Body length, body weight and walking activity of larvae

The body length and body weight of the four instars of *C. transversalis* were significantly higher than those of *P. dissecta* (Table I). The walking activity of first instar *P. dissecta* was greater than that of *C. transversalis*. However, the walking activity of second, third and fourth instars of *P. dissecta* was less than of *C. transversalis*

Table I. Body length, body weight and speed of walking in four larval stages (L₁–L₄) of *P. dissecta* and *C. transversalis*.

| Parameter | Larval stage | <i>P. dissecta</i> | <i>C. transversalis</i> | F value |
|------------------------------|----------------|--------------------|-------------------------|----------|
| Body length (in mm) | L ₁ | 1.9±0.2 | 2.6±0.4 | 19.60** |
| | L ₂ | 4.8±0.3 | 5.6±0.7 | 10.49* |
| | L ₃ | 6.6±0.5 | 7.6±0.8 | 11.54* |
| | L ₄ | 8.2±0.6 | 9.6±1.0 | 13.31* |
| Body weight (in mg) | L ₁ | 1.6±0.1 | 2.2±0.1 | 84.90** |
| | L ₂ | 3.1±0.2 | 5.4±0.2 | 542.51** |
| | L ₃ | 6.0±0.5 | 9.8±0.2 | 532.64** |
| | L ₄ | 13.2±0.7 | 19.8±0.2 | 796** |
| Speed of walking (in cm/min) | L ₁ | 40.6±9.7 | 25.2±1.2 | 25.03** |
| | L ₂ | 55.9±3.9 | 77.5±6.8 | 76.15** |
| | L ₃ | 87.8±1.9 | 112.0±3.5 | 395.73** |
| | L ₄ | 107.0±19.3 | 123.1±4.0 | 6.70* |

Values are mean±SD. Significant at: * $P < 0.01$; ** $P < 0.0001$; Tukey's test: range = 2.97; d.f. = 1,18.

(Table I). Thus, *C. transversalis* larvae were bigger, heavier and faster than *P. dissecta* at all stages except first instar *P. dissecta*, which though smaller and lighter, were faster than *C. transversalis*.

Attack, escape and predation rates of larvae

The attack rate of larvae of *C. transversalis* was greater towards conspecific (73%) than to heterospecific (42%) larvae ($F = 10.25$; $P < 0.001$; d.f. = 3,20; Figure 1). Similarly, the attack rate of *P. dissecta* was greater toward conspecific (50%) than to heterospecific (27%) larvae, and were less than that of *C. transversalis* (Figure 1). All instars of *C. transversalis* attacked *P. dissecta* of the same stage and younger (Figure 2). However, no *C. transversalis* were attacked by *P. dissecta* of the same stage (Figure 2). The attack rates were highest for third instars of both species.

The escape rates were significantly higher ($F = 20.59$; $P < 0.001$; d.f. = 3,20) for *C. transversalis* from conspecifics (65%) and heterospecific predators (80%). *Propylea dissecta* made fewer escapes from both conspecifics (27%) and heterospecifics (24%). In *P. dissecta*, second instars made the greatest number of escapes after being attacked by conspecific or heterospecific predators of the same stage, while the third instars made the most escapes when attacked by older conspecifics (Figure 3). In *C. transversalis*, all four larval instars made high number of escapes from cannibals and heterospecific predators.

Larvae of *P. dissecta* were the most likely among the two species tested to act as cannibals, with conspecific predation rates of 66%. This was followed by predation of *P. dissecta* by *C. transversalis* (31%), revealing the latter to be a significantly ($F = 5.79$; $P < 0.001$; d.f. = 3,20) better intraguild predator. *Coccinella transversalis* was less likely to act as a cannibal with conspecific predation rates of 24% (Figure 1). Among the larval stages, first instars of *P. dissecta* were consumed more by conspecifics and heterospecifics of the same instar and older (Figure 4). For *C. transversalis*, more first instars were consumed than later instars by cannibals. No larvae of *C. transversalis* were eaten by *P. dissecta* of the same stage.

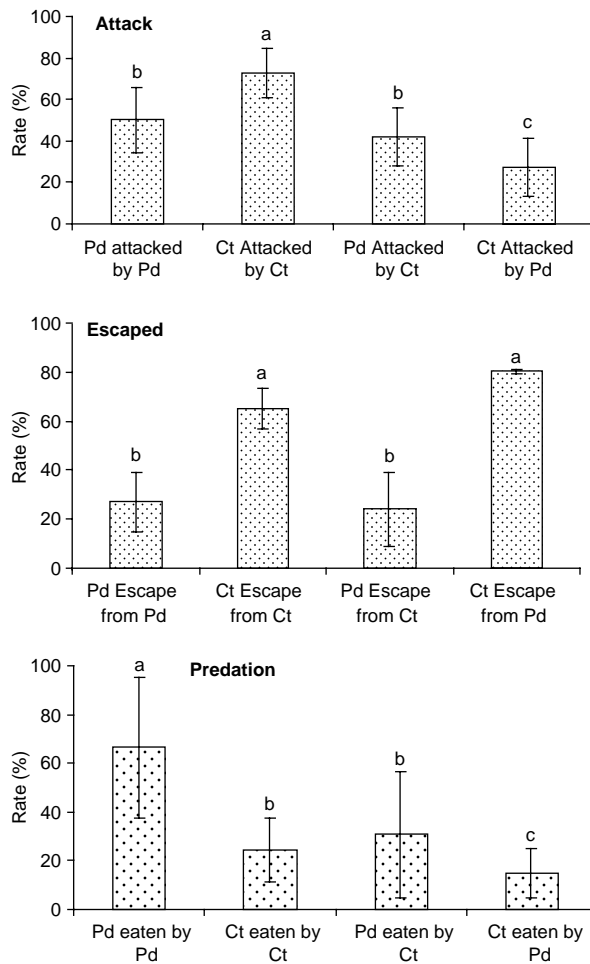


Figure 1. Percent attack, escape and predation by the larvae of two ladybird species, *P. dissecta* and *C. transversalis*. Different letters denote that data are significant at $P < 0.05$ (Fisher's PLSD). All instars Pooled.

Discussion

The results revealed that predators differed in their size and walking activity. Larvae of *C. transversalis* were bigger and heavier than *P. dissecta*. With an exception of first instars, the larvae of *C. transversalis* were faster than those of *P. dissecta*. It is likely that increased size and walking activity increases the probability of acting as a conspecific or heterospecific predator (Agarwala et al. 2003). All four instars of *P. dissecta* and *C. transversalis* can indulge in cannibalism and IGP in absence of essential prey. However, the incidence of cannibalism and IGP differed within and between the species. *Propylea dissecta* appears more evolved as a cannibal with a high tendency of attacking and consuming conspecifics. This lends support to our previous finding that cannibalism is more preferred in *P. dissecta* than *C. transversalis* (Omkar et al. 2004). Predation rate of first instar *P. dissecta* was greater by conspecifics of same

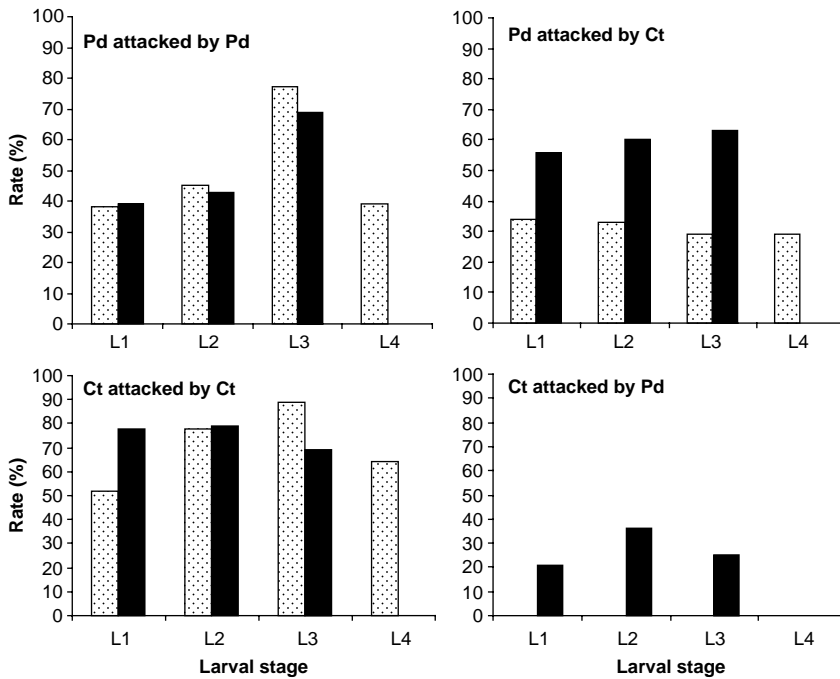


Figure 2. The percent individuals attacked by the conspecific and heterospecific larvae of *P. dissecta* and *C. transversalis*. Dotted bars – predation by the same instar; black bars – predation by older instar.

and older instars. This indicates that cannibalism of first instars could be higher in the field. This is adaptive, as it will ensure the survival and development of some of the individuals feeding on inferior conspecifics under stress of prey scarcity. The resulting adults could then fly and search for more suitable habitat for mating and oviposition (Kindlmann & Dixon 1993). This also suggests that earlier instars of *P. dissecta* are more likely to secure their progeny and gene pool, and are better evolved cannibals. It is likely that if a smaller ladybird is maintaining a stable coexistence with the larger species, then it must be gaining some intrinsic advantages which are compensating for the costs of reduced size (Omkar et al. 2005).

Larvae of *C. transversalis* attacked both conspecifics and heterospecifics. However, due to high escape rates of conspecific larvae, cannibalism generally was not favored. Whereas, in *P. dissecta*, though relatively fewer individuals were attacked, most of them were cannibalized due to lower escape rates of victims. This suggests that as a potential cannibal, *P. dissecta* is superior to *C. transversalis*.

In most of the cases where a larva of *C. transversalis* was one-instar older than *P. dissecta*, it dominated the intraguild combats and consumed the latter. However, when at same instar, there were only few incidences of predation by *C. transversalis*. Larvae of *P. dissecta* made fewer attempts to attack and consume the younger heterospecific larvae and most failed to consume it due to high escape rates of the latter. Collectively, this suggests that *P. dissecta* larvae were most often intraguild prey of *C. transversalis*. *Coccinella septempunctata* (*Cs*) had become an intraguild prey to *H. axyridis* (*Ha*) due greater attack (less than 20% in *Cs* and more than 50% in *Ha*) and predation (less than 5% in *Cs* and more than 50% in *Ha*) rates of the latter in the laboratory (Yasuda et al. 2001).

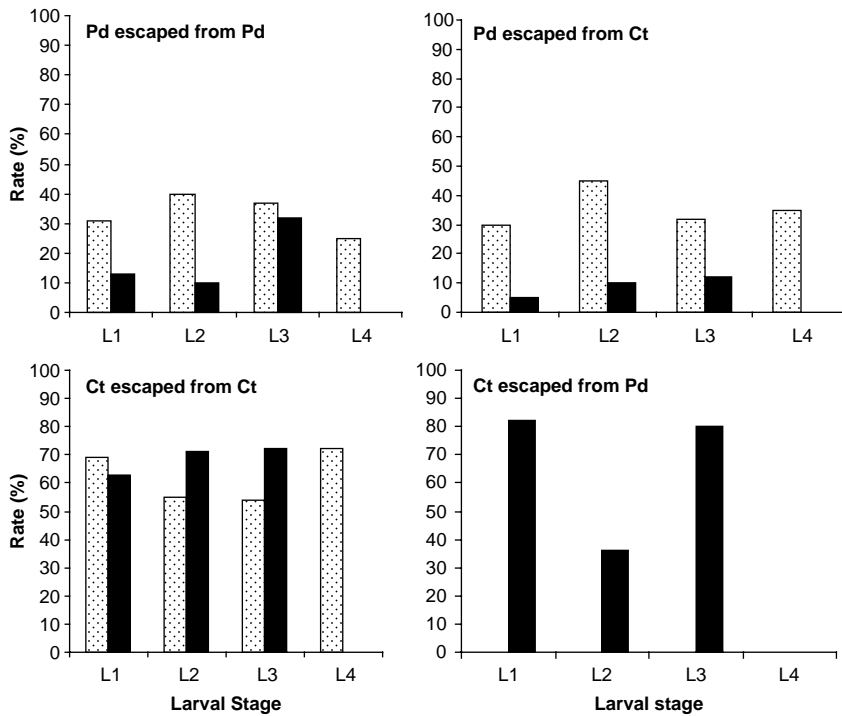


Figure 3. The percent individuals escaped from the conspecific and heterospecific larvae of *P. dissecta* and *C. transversalis*. Dotted bars – predation by the same instar; black bars – predation by older instar.

In a recent study, 60% mortality of *Propylea japonica* (Thunberg) larvae was largely due to cannibalism and intraguild predation by the ladybirds, *H. axyridis* and *Coccinella septempunctata brucki* Mulsant when all three ladybirds were interacting in a prey-scarce condition (Sato et al. 2003). We found behavior of *P. dissecta* very similar to that of *P. japonica* (Sato et al. 2003), as larvae of both these species were easily attacked and preyed upon by superior conspecifics and heterospecifics in prey scarcity. The survival of *C. s. brucki* larvae was not affected by the other two species due to their early emigration which might have enabled them to escape intraguild predation by *H. axyridis* (Sato et al. 2003). The escape behavior also prevented cannibalism in *C. s. brucki* larvae, which was similar to the behavior of *C. transversalis* in the present study. In North America, the indigenous ladybirds, *Coccinella transversoguttata* Brown and *Hippodamia convergens* Guerin-Meneville became intraguild prey, as they were least successful in escaping the attacks of an introduced species, *H. axyridis* (Snyder et al. 2004; Yasuda et al. 2004). Older larvae of *H. axyridis* had especially strong negative effects on younger larvae of indigenous ladybirds (Yasuda et al. 2004), which supports our findings that predation rate increases when younger and older instars interacted. The ladybird, *Adalia bipunctata* L. is treated as intraguild prey by *H. axyridis* and *C. septempunctata* leading to the failures of establishing former in Japan (Sato & Dixon 2004).

Mobility and body weight were the main factors affecting the magnitude of intraguild predation in *H. axyridis* and *Coccinella undecimpunctata* L. (Felix & Soares 2004). However, a small difference in body weight led to a marked increase in rate of

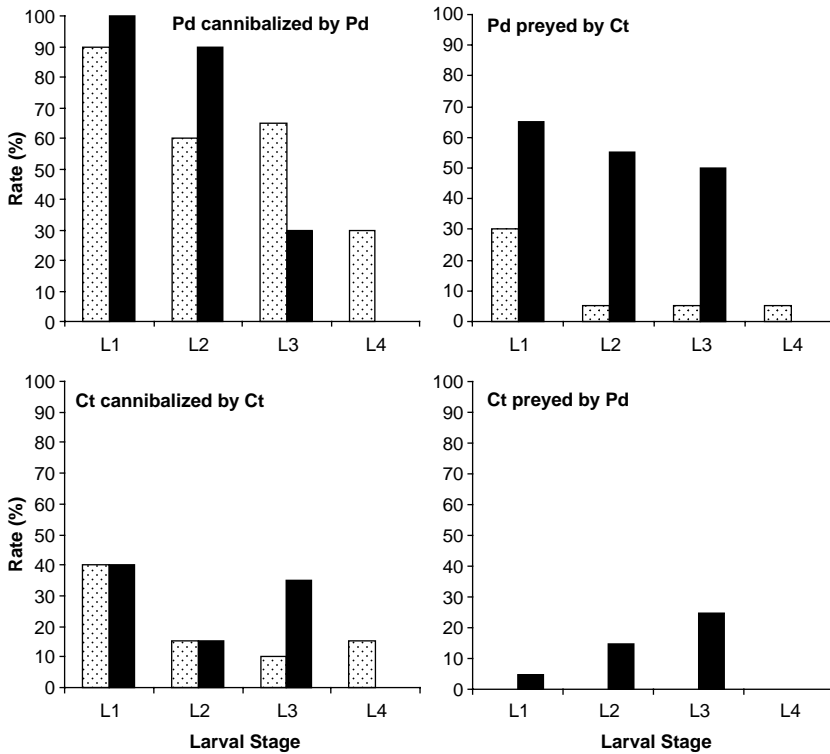


Figure 4. The percent individuals cannibalized and preyed upon by the larvae of *P. dissecta* and *C. transversalis*. Dotted bars – predation by the same instar; black bars – predation by older instar.

predation for *H. axyridis* but not for *C. undecimpunctata*. Our study supports the findings of Felix and Soares (2004), as there was a marked increase in rate of predation in *C. transversalis* but not in *P. dissecta* when the same larval stage was used.

The relatively aggressive behavior of hungry larvae of *C. transversalis* towards *P. dissecta* is largely attributed to their relative sizes, as all four larval stages of *C. transversalis* were bigger than *P. dissecta*. This was also supported by the fact that incidence of conspecific and heterospecific predation was usually higher when the attacker was one instar older, and thus was bigger in size than victim. Size disparity is known to have a large effect on conspecific and heterospecific predation (Agarwala & Dixon 1992; Snyder & Hurd 1995; Lucas et al. 1997; Gagne et al. 2002; AP, O and AKG, unpublished data). In most ladybird species examined, the older larvae move faster than young ones (Ng 1988). Thus, it is likely easier for fast moving older instars to attack and consume the younger instars. In addition, it is largely known that the bioconversion efficiency of older instars is less than that of younger ones, which suggests that the former feed more and convert less prey biomass into predator biomass because of high metabolic cost (Baumgartner et al. 1987). Thus, there is more pressure for food intake in the older instars. This pressure could drive the older instars to increasingly indulge in cannibalism and intraguild predation.

Prey specificity is also a factor, which might have affected the outcome of heterospecific interactions (Strand & Obrycki 1996). It is likely that specialist predators could become prey in intraguild interactions to a predator having a

relatively wide prey range (Lucas et al. 1998). This factor could also be a possible reason for the decline of *C. septempunctata* by *H. axyridis* as the latter is more polyphagous (Lucas et al. 1997; Yasuda & Ohnuma 1999). The present study corroborates earlier findings that *P. dissecta* generally has a more limited prey range than *C. transversalis* (Omkar & Pervez 2004; Pervez & Omkar 2004a).

Our laboratory data provide insight into the complex phenomena occurring in the fields. Though both *C. transversalis* and *P. dissecta* maintain a stable coexistence when aphids are abundant, it is likely that in times of prey scarcity and in patchy prey habitats, the former species may dominate the guild, and may become a threat to the immature stages of *P. dissecta*. Further studies are needed to test the outcome of these interactions in field conditions. Thus, it could be concluded that: (i) attack and escape rates of larvae of *C. transversalis* were higher than those of *P. dissecta* toward both conspecific and heterospecific victims, (ii) third instars of both species exhibited the greatest tendency to attack, (iii) cannibalistic tendencies were stronger in *P. dissecta*, especially in first instars compared to later instars, (iv) larvae one instar older than their opponent generally attacked and consumed the inferior conspecific or heterospecific larvae, and (v) *P. dissecta* was most often intraguild prey for *C. transversalis*.

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