Inter- and intraspecific interactions in two mealybug predators *Spalgis epius* and *Cryptolaemus montrouzieri* in the presence and absence of prey

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Abstract

Spalgis epius and *Cryptolaemus montrouzieri* are the two potential predators of different species of mealybugs. However, the mode of their interactions is not known to use these predators together in the field. Hence, we investigated on the possible interactions i.e., cannibalism, intraguild predation (IGP) and competition between the predators in the presence and absence of prey *Planococcus citri*. In the presence of prey, no cannibalism and predation were observed in both *S. epius* and *C. montrouzieri* larvae. A pair of *S. epius* larvae consumed significantly more number of mealybugs than one *S. epius*/*C. montrouzieri* larva or a pair of *C. montrouzieri* larvae. The predation of *S. epius* larva by *C. montrouzieri* larva was significantly more than the predation of *C. montrouzieri* by *S. epius*. Conspecific and interspecific egg predation was absent both in *S. epius* and *C. montrouzieri*. Cannibalism in *C. montrouzieri* was more than that in *S. epius*. The study indicated that *C. montrouzieri* larvae can be used as an additive along with voracious *S. epius* larvae under abundant prey population. IGP was asymmetric between the two predators in the absence of prey. Both *S. epius* and *C. montrouzieri* larvae can maintain a stable coexistence when prey is abundantly available, however, in the complete absence of prey *C. montrouzieri* may dominate the guild. This study provides an insight into the possible complex inter- and intraspecific predatory phenomena in the field to use these two predators in the biological control of mealybugs.

Keywords: inter- and intraspecific interactions, cannibalism, intraguild predation, *Spalgis epius*, *Cryptolaemus montrouzieri*, *Planococcus citri*

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Introduction

Fundamental question in biological control is how multiple predators interact collectively to suppress the populations of herbivorous pests (Denoth *et al.*, 2002; Wilby & Thomas, 2002; Symondson *et al.*, 2002; Cardinale *et al.*, 2003; Mills, 2006).

Inter- and intraspecific competitions are important interactions among organisms which share the same food. Cannibalism and intraguild predation (IGP) have attracted much attention as these interactions are significant and widespread among many taxa of predatory arthropods. In biological communities, complex interactions and more specifically cannibalism and IGP are considered as key determinants of population dynamics and community structure (Polis & Holt, 1992; Wagner & Wise, 1996; Holt & Polis, 1997). Cannibalism and IGP determine the fate of a community (Godfray & Pacala, 1992). IGP could be either symmetric when species are mutual predators of one another or

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asymmetric when one species consistently prey upon the other (Polis *et al.*, 1989). Thus, IGP may have a negative effect on the outcome of biological control (Snyder & Ives, 2001; Rosenheim, 2005). However, studies have shown that the incidence of IGP could have a positive effect on biocontrol of pests (Schausberger & Walzer, 2001; Snyder *et al.*, 2004; Gardiner & Landis, 2007). In pest management, usage of multiple predators remains contentious, as there are extensive data both for and against the suppression of pest populations (Denno & Finke, 2006). There are evidences showing that multiple natural enemies can exert a strong collective control on agricultural pests (Symondson *et al.*, 2002; Cardinale *et al.*, 2003). Yet, some studies confirmed that employing multiple agents to control pest herbivores disrupt biological control (Snyder & Ives, 2001; Prasad & Snyder, 2004). The ability of a natural enemy complex to curtail a pest population is depending on the strength of interactions among themselves. There is a possibility that multiple predators may interact synergistically to enhance pest suppression (Losey & Denno, 1999) or their effects on pest populations are simply additive when they do not interact at all (Chang, 1996; Straub & Snyder, 2006). However, some species of predators may interact antagonistically wherein they consume each other, which affect pest control (Finke & Denno, 2003; Prasad & Snyder, 2004). A few are known about the basic components of these interactions, which are directly associated with cannibalism and IGP in ladybird beetles (Yasuda *et al.*, 2001). Thus, in a biological control perspective it becomes essential to critically assess the nature of interactions (i.e., antagonistic, synergistic or no interaction between predators), the frequency and strength of such interactions in the food web, how such interactions affect pest suppression, and how habitat and landscape structures might rage predator-predator interactions (Denno & Finke, 2006).

Several species of mealybugs (Hemiptera: Pseudococcidae) are serious pests on various crops e.g., coffee, citrus, cocoa, guava, grapes, papaya, cotton, mango, mulberry, vegetable crops, ornamental plants, etc. worldwide (Browning, 1992; Franco *et al.*, 2001; Dinesh & Venkatesha, 2011*a*, *b*). Mealybugs possess a protective wax body coating and have the ability of being protected inside bark crevices and other inaccessible parts of plants; hence satisfactory control measures have not been achieved with insecticides (Joyce *et al.*, 2001). Thus, management of mealybugs by biological control provides a sustainable and efficient control approach (Bentley, 2002).

The apefly *Spalgis epius* (Westwood) (Lepidoptera: Lycaenidae) is a potential predator of different species of mealybugs (Dinesh & Venkatesha, 2011*a*,*b*). *S. epius* occurs in India, Burma, Sri Lanka, Philippines, Java, Bangladesh, Thailand and Krakatau Island (Indonesia) (see Dinesh & Venkatesha, 2011*a*). Studies on the biology, development, mating and egg laying behaviour, feeding potential and mass rearing of *S. epius* have been conducted (Venkatesha *et al.*, 2004, 2005; Venkatesha & Shashikumar, 2006; Dinesh *et al.*, 2010; Dinesh & Venkatesha, 2011*a*,*b*, 2012, 2013*a*,*b*; Venkatesha & Dinesh, 2011). *S. epius* has four larval instars and completes its life cycle in 23.8 days at laboratory condition (Dinesh *et al.*, 2010).

Another mealybug predator *Cryptolaemus montrouzieri* Mulsant (Coleoptera: Coccinellidae) is one of the most widely used natural enemies of mealybugs (Heidari & Copland, 1992; Perez-Jaggi, 1995). Both adults and larvae of *C. montrouzieri* actively search for prey on vegetation and consume all stages of mealybugs (Clausen, 1978). *C. montrouzieri* has four larval

instars and completes its life cycle in 28.4 days at laboratory condition (Mani & Thontadarya, 1987).

S. epius and *C. montrouzieri* found to coexist in agricultural fields sharing common prey resources (Mani, 1995). Although both the predators are considered as potential predators of various species of mealybugs, no information is available about their interactions in the presence and absence of a prey species to utilize these predators together in the field as biocontrol agents against mealybugs. Hence, a study was carried out to explore the role of IGP, cannibalism and competition as possible mechanisms to understand a relationship between these two predators. Further, to assess whether the combination of these two major predators could result in a better biological control of mealybugs in the field, we tested their voracity on mealybugs.

Materials and methods

Laboratory rearing of S. epius and C. montrouzieri

To rear *S. epius* and *C. montrouzieri* in the laboratory, their host mealybug *Planococcus citri* (Risso) was cultured on pumpkins (*Cucurbita maxima* Duchesne) as described by Serrano & Lapointe (2002). *S. epius* and *C. montrouzieri* were reared separately on the mealybug-infested pumpkins at $28 \pm 1°C$, $65 \pm 5\%$ RH and photoperiod 12:12 L:D in an environment chamber following the methods of Chacko *et al.* (1978) and Venkatesha & Dinesh (2011). All experiments were conducted at $28 \pm 1°C$, $65 \pm 5\%$ RH and photoperiod 12:12 L:D in an insect environment chamber.

Interaction and voracity of two predators

To study the interaction and prey consumption of *S. epius* and *C. montrouzieri*, plastic cups (5 cm diameter) with cut-opened bottom were fixed on the surface of a pumpkin using melted paraffin wax and this served as an arena for the experiment. Through the open end of the cup, 200 mealybug crawlers (first instar nymphs) were released on the pumpkin and the mouth of the cup was closed using muslin cloth. When nymphs reached the adult stage, the number of adult mealybugs present inside the cup was counted and the newly hatched first instar larva of *S. epius* and *C. montrouzieri* were released into the cup in three different combinations: (a) one larva each of *S. epius* and *C. montrouzieri*, (b) two larvae of *C. montrouzieri*, and (c) two larvae of *S. epius*. Observations were made on inter- and intraspecific larval interactions, their feeding behaviour and the number of prey consumed in the three combinations. Observations were made daily 5–6 times for about 2 h at an interval of 3–4 h until all the larvae pupated. Each experiment was replicated five times with ten trials per replication.

Interspecific interaction in the absence of prey

All the four larval instars of *S. epius* and *C. montrouzieri* were collected from mealybug-infested pumpkins and kept individually in Petri dishes (5 cm diameter). These larvae were starved for 12 h to induce hunger. Larvae of identical age and size were used based on the day of their ecdysis. In the first set of experiment, to investigate interactions between the similar instar larvae of *S. epius* and *C. montrouzieri*, a single first instar larva of both *S. epius* and *C. montrouzieri* were transferred to a clean Petri dish (5 cm diameter) at opposite poles with the

help of a single-bristle paintbrush. The mode of interaction between the two larvae was recorded after 24 h. Similarly, experiments were conducted for the second, third and fourth instar larvae of the two predators. Each combination was replicated 50 times.

In the second set of experiment, IGP studies were conducted in two different combinations: (a) younger instar larva of *S. epius* vs. one instar older larva of *C. montrouzieri* (i.e., I instar *S. epius* larva vs. II instar *C. montrouzieri* larva, II instar *S. epius* larva vs. III instar *C. montrouzieri* larva, and III instar *S. epius* larva vs. IV instar *C. montrouzieri* larva) and (b) younger instar larva of *C. montrouzieri* vs. one instar older larva of *S. epius* (i.e., I instar *C. montrouzieri* larva vs. II instar *S. epius* larva, II instar *C. montrouzieri* larva vs. III instar *S. epius* larva, and III instar *C. montrouzieri* larva vs. IV instar *S. epius* larva). Based on the day of larval ecdysis, larval instars were determined and utilized in the experiment. In all combinations one larva of each predator was used. Each experiment was replicated 50 times. Larvae were transferred to a Petri dish at opposite poles and the modes of interactions were recorded after 24 h.

Intraspecific interaction in the absence of prey

In the first set of experiment, intraspecific interactions were studied both in *S. epius* and *C. montrouzieri*. Two first instar *S. epius* larvae of identical age and size were transferred to a Petri dish at opposite poles, and the type of interaction between them was noted after 24 h. Similarly, experiments were conducted for the second, third and fourth instar larvae of *S. epius* and *C. montrouzieri* separately. Each larval combination was replicated five times with ten trials per replication.

In the second set of experiment, intraspecific interaction studies were conducted in two different combinations: (a) younger instar larva of *S. epius* vs. one instar older larva of *S. epius* (i.e., I instar larva vs. II instar larva, II instar larva vs. III instar larva, and III instar larva vs. IV instar larva) and (b) younger instar larva of *C. montrouzieri* vs. one instar older larva of *C. montrouzieri* (i.e., I instar larva vs. II instar larva, II instar larva vs. III instar larva, and III instar larva vs. IV instar larva). In all combinations a newly moulted single larva from each instar of the predators was used. Larvae were transferred to a Petri dish at opposite poles and the modes of interactions were recorded after 24 h. Each experiment was replicated five times with ten trials per replication. The percentage of cannibalism was calculated in each combination for both the predators.

Egg, prepupa and pupal predation/cannibalism

Egg, prepupa and pupal predation/cannibalism studies were conducted in five different combinations: (a) ten eggs of *S. epius* vs. one I/II/III/IV instar larva of *S. epius*, (b) ten eggs of *C. montrouzieri* vs. one I/II/III/IV instar larva of *C. montrouzieri*, (c) ten eggs of *S. epius* vs. one I/II/III/IV instar larva of *C. montrouzieri*, (d) ten eggs of *C. montrouzieri* vs. one I/II/III/IV instar larva of *S. epius*, and (e) ten eggs, one larva each from four larval instars, one prepupa and one pupa of *S. epius* independently vs. one adult of *C. montrouzieri*. As *S. epius* adults are non-predacious and feed on nectar/water, they were not utilized in the experiment like *C. montrouzieri* adults. Thus, there were eight intraspecific and 15 interspecific

combinations. Each experiment was replicated five times with ten trials per replication.

Data analysis

The outcome of interspecific interactions was classified as: *S. epius* acted as an intraguild (IG) prey, *S. epius* acted as an IG predator or no incidence of IGP occurred. For each species-pair comparison, the level of IGP between *S. epius* larvae and *C. montrouzieri* larvae was determined as the proportion of replicates in which IGP occurred out of the total number of replicates for that combination. Following the method of Lucas *et al.* ([1998](#)) an index of symmetry was measured by the proportion of replicates in which *S. epius* was the IG predator out of the total number of replicates wherein IGP occurred. Thus, a symmetry index of >0.5 IGP was in favour of *S. epius*, while an index of <0.5 IGP was in favour of *C. montrouzieri*. The symmetry indices for each combination were compared with the theoretical index of 50% corresponding to a symmetrical interaction, using a Chi-square test (χ^2, $P < 0.05$) (SPSS Inc. [2008](#)). The symmetry of IGP between *S. epius* and *C. montrouzieri* at different larval instar was analysed by using the binomial test, the null hypothesis being that predation is equally likely to occur in both the ways. The strength of IGP between the two species of predators for a given combination was assessed using the χ^2 test with an expected value of 50% and was considered (i) symmetrical, when the χ^2 value was not significant, wherein the rate of predation of the two predators was similar, (ii) asymmetrical, when the χ^2 value was significant, in which the rate of predation of the two predators was different, and (iii) not significantly asymmetrical, when the χ^2 value was not significant, wherein the rate of predation of the two species not much differed.

The voracity of larvae in different combinations was subjected to analysis of variance (ANOVA). When ANOVA was significant at the $P < 0.05$ level, differences were determined by *post hoc* Tukey's HSD (Honestly Significant Difference) multiple range test at probability level $P < 0.05$ as significant (SPSS Inc. [2008](#)). The percentage of cannibalism in each experimental combination and overall predation (i.e., pooled data of the percentage of predation/cannibalism) in both species were arcsin transformed and subjected to non-parametric analysis of variance using Kruskal–Wallis test. A non-parametric approach was used because of heteroscedasticity and departures from normality (Zar, [1984](#)). When significant difference was found in Kruskal–Wallis test at the $P < 0.05$ level, multiple pairwise Mann–Whitney U test was used to know the differences in the cannibalism in different larval instars of each predator and overall predation and cannibalism in both the predators. Alpha values were adjusted according to the Bonferroni correction for multiple comparisons (referred to in text as αB).

Results

Interaction and voracity of two predators

In the presence of prey, no cannibalism and predation were observed both in *S. epius* and *C. montrouzieri* larvae. When *C. montrouzieri* and *S. epius* larvae were maintained together, they fed on prey at different places in the arena. *S. epius* larva was found feeding continuously throughout its development, whereas *C. montrouzieri* larva was feeding and resting at times. A pair of *S. epius* larvae consumed more

Table 1. Interspecific interaction between *Spalgis epius* and *Cryptolaemus montrouzieri*.

Species/larval instar	*Spalgis epius* acts as prey	*Spalgis epius* acts as predator	Level of IGP	Symmetry of IGP
I instar Se vs. I instar Cm	15	5	0.4	0.25
II instar Se vs. II instar Cm	25	5	0.6	0.16
III instar Se vs. III instar Cm	15	10	0.5	0.40
IV instar Se vs. IV instar Cm	5	5	0.2	0.50
	Younger *Spalgis epius* acts as prey	Younger *Spalgis epius* acts as predator	Level of IGP	Symmetry of IGP
I instar Se vs. II instar Cm	35	0	0.7	0
II instar vs. III instar Cm	16	0	0.3	0
III instar vs. IV instar Cm	11	6	0.3	0.35
	Older *Spalgis epius* acts as prey	Older *Spalgis epius* acts as predator	Level of IGP	Symmetry of IGP
I instar Cm vs. II instar Se	10	5	0.3	0.33
II instar Cm vs. III instar Se	30	6	0.7	0.16
III instar Cm vs. IV instar Se	6	0	0.1	0

Se- *Spalgis epius*. Cm- *Cryptolaemus montrouzieri*. $N = 50$ for each pairing.

number of mealybugs compared to one larva of *S. epius*/ *C. montrouzieri* or two larvae of *C. montrouzieri* ($F_{2, 12} = 545.14$; $P < 0.05$) (fig. 1).

Interspecific interaction in the absence of prey

The level and symmetry index of IGP between *S. epius* and *C. montrouzieri* from first to fourth instar larvae is presented in table 1. In interactions between the similar larval instars of two predators, IGP was significantly asymmetrical and in favour of *C. montrouzieri* in the first ($\chi^2_1 = 5$; $P < 0.05$) and second instar larvae ($\chi^2_1 = 13.3$; $P < 0.05$) (fig. 2A). Whereas, IGP was symmetrical in the third ($\chi^2_1 = 1$; $P = 0.317$) and fourth ($\chi^2_1 = 0$; $P = 1$) larval instar combinations of the two predators (fig. 2A).

In interactions between younger *S. epius* and older *C. montrouzieri* larval instars, IGP was significantly asymmetrical and exclusively in favour of older *C. montrouzieri* against the first ($\chi^2_1 = 35$; $P < 0.05$) and second ($\chi^2_1 = 16$; $P < 0.05$) instar larvae of *S. epius*. IGP was not significantly asymmetrical between the third instar larva of *S. epius* and the fourth instar larva of *C. montrouzieri* ($\chi^2_1 = 1.47$; $P = 0.225$) (fig. 2B).

In interactions between older *S. epius* and younger *C. montrouzieri* larval instars, IGP was not significantly asymmetrical between the second instar larva of *S. epius* and the first instar larva of *C. montrouzieri* ($\chi^2_1 = 1.6$; $P = 0.196$). Whereas, IGP was significantly asymmetrical and in favour of younger *C. montrouzieri* against the third ($\chi^2_1 = 16$; $P < 0.05$) and fourth ($\chi^2_1 = 6$; $P < 0.05$) instar larvae of *S. epius* (fig. 2C).

Intraspecific interaction in the absence of prey

In intraspecific interactions between the same larval instars of *S. epius*, cannibalism was significantly different among four larval instars ($H_3 = 14.35$; $P < 0.05$). Cannibalism was maximum in the third instar larva compared to other larval instars, and it was significantly different from the first (αB 6 tests; $P = 0.008$) ($U = 0.00$; $P = 0.006$) and fourth ($U = 0.00$; $P = 0.007$) instar larvae (fig. 3A). Similarly, in *C. montrouzieri* there were significant differences in cannibalism among different larval
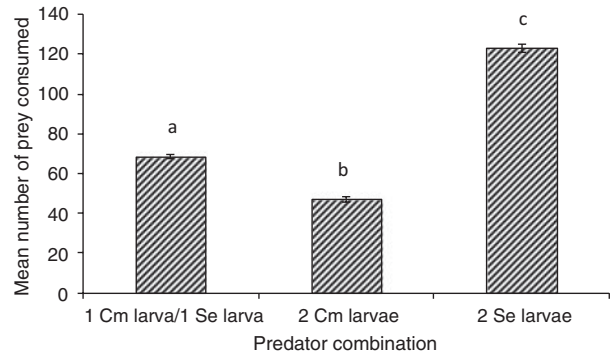

Fig. 1. Mean (±SE) voracity of *Spalgis epius* (Se) and *Cryptolaemus montrouzieri* (Cm) larvae. Bars with different letters indicate the significant difference in the number of prey consumed (ANOVA; Tukey HSD test $P < 0.05$). Vertical lines indicate the SE of the mean number of prey consumed.

instars ($H_3 = 15.84$; $P < 0.05$). Cannibalism was greater in the first and second instar larvae than in the third and fourth instar larvae ($P < 0.008$) (fig. 3B).

In conspecific interactions between young and one instar older larva of *S. epius*, cannibalism was significantly different in different larval instars of *S. epius* (i.e., older larval instars cannibalized on younger larval instars: $H_2 = 11.29$; $P < 0.05$ and younger larval instars cannibalized on older larval instars: $H_2 = 11.35$; $P < 0.05$). The third instar larva of *S. epius* was significantly more cannibalistic both on second (αB 3 tests; $P = 0.016$) ($U = 0.00$; $P = 0.005$) and fourth instar larvae ($U = 0.00$; $P = 0.006$) than other larval instars (fig. 4A). Whereas, the second instar larva of *C. montrouzieri* was significantly more cannibalistic on first instar larva than other larval instars ($H_2 = 10.72$; $P < 0.05$) (αB 3 tests; $P = 0.016$) ($U = 0.00$; $P = 0.007$) (fig. 4B). Cannibalism by younger larva on older *C. montrouzieri* larva was minimum and there were no significant differences among different larval instars ($H_2 = 4.04$; $P = 0.132$) (fig. 4B).
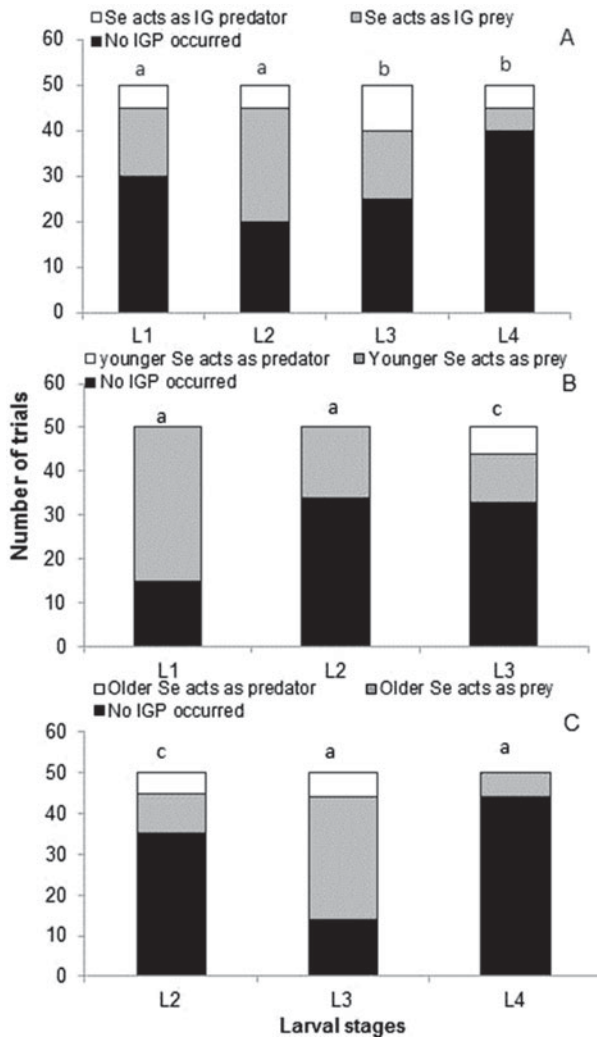
Fig. 2. Symmetry of IGP between *Spalgis epius* and *Cryptolaemus montrouzieri*. (A) IGP between similar instar larvae, (B) IGP between younger *S. epius* and older *C. montrouzieri* larvae and (C) IGP between older *S. epius* younger *C. montrouzieri* larvae. Analysis shows that larval instars marked a, IGP was asymmetric; larval instars marked b, IGP was symmetric; and larval instars marked c, IGP was not significantly asymmetric.

Overall predation/cannibalism

Overall predation between *S. epius* larva and *C. montrouzieri* larva was significantly different ($H_3 = 64.47$; $P < 0.05$). Overall predation of *S. epius* larva by *C. montrouzieri* larva was significantly more than that of *C. montrouzieri* by *S. epius* (αB 6 tests; $P = 0.008$) ($U = 147.0$; $P < 0.0001$) (fig. 5). Overall cannibalism was more in *C. montrouzieri* larva than that in *S. epius* larva and it was not significantly different ($U = 987.0$; $P = 0.062$) (fig. 5).

Egg, prepupa and pupal predation/cannibalism

Conspecific and interspecific egg predations were absent both in *S. epius* and *C. montrouzieri* larvae in the absence and presence of prey. *C. montrouzieri* adults predated on all larval
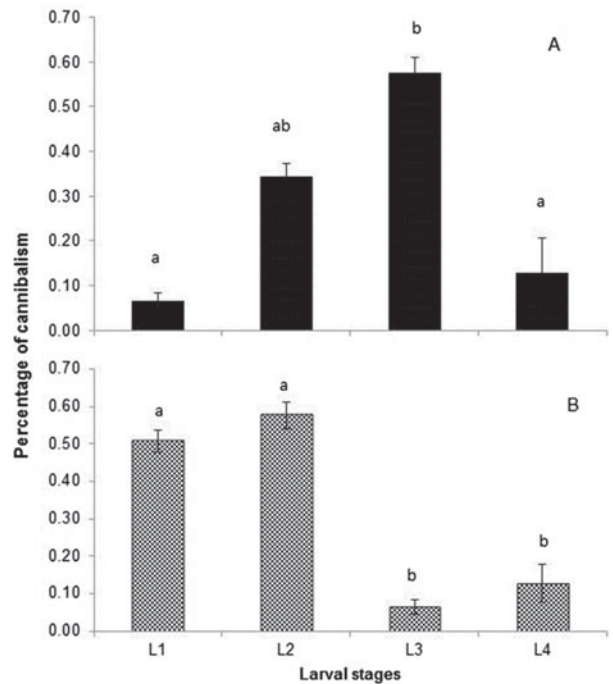

Fig. 3. Mean (±SE) percentage of cannibalism in the same larval instars of *Spalgis epius* (Se) and *Cryptolaemus montrouzieri* (Cm) in the absence of prey. (A) Se cannibalized by Se, (B) Cm cannibalized by Cm. Bars with different letters indicate the significant difference in the percentage of cannibalism (Mann–Whitney *U* test αB $P < 0.008$). Vertical lines indicate the SE of the mean number of percentage of cannibalism.

instars, prepupa, and fresh pupa of *S. epius* in the absence of prey. Except the first instar larva of *S. epius* and *C. montrouzieri*, all larval instars of both the predators attacked the prepupa and fresh pupa of *S. epius* in the absence of prey. In *C. montrouzieri* no larval instars attacked conspecific pupa.

Discussion

The results of our study indicated that no cannibalism and predation exist both in *S. epius* and *C. montrouzieri* in the presence of prey. *S. epius* is known to deposit a maximum number of eggs on the mealybug-infested pumpkins containing conspecific eggs (Dinesh & Venkatesha, 2013b), which may be because of the absence of egg/larval cannibalism. Maximum prey consumption in combination of two *S. epius* larvae may be due to their voracious and continuous feeding habit. Thus, *S. epius* could be a potential predator of mealybugs as reported by Dinesh and Venkatesha (2011a, b). When *S. epius* larvae voraciously fed on the main mass of mealybugs, *C. montrouzieri* larvae cleared leftover eggs, nymphs, and half-eaten adults of mealybugs from the margin. The coexisting feeding behaviour of these two predators could be additive in the suppression of pest populations. Larvae of both *S. epius* and *C. montrouzieri* known to coexist in agricultural fields sharing common prey resources and successfully reducing prey populations (Mani, 1995).

IGP and cannibalism are two important mortality factors in predators and these could be a regulatory mechanism
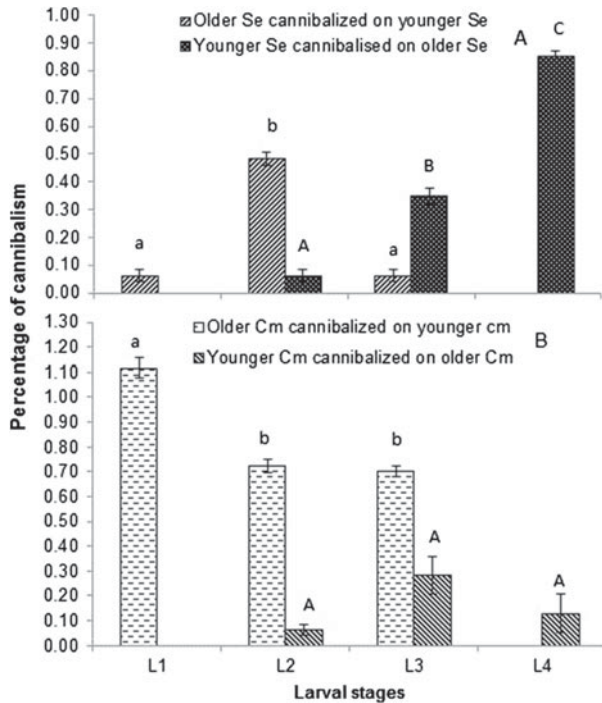
Fig. 4. Mean (±SE) percentage of cannibalism in different larval instars of *Spalgis epius* (Se) and *Cryptolaemus montrouzieri* (Cm) in the absence of prey. (A) older and younger Se cannibalized on younger and older Se, (B) older and younger Cm cannibalized on younger and older Cm. Bars with different letters indicate the significant difference in the percentage of cannibalsm (Mann–Whitney *U* test αB *P*<0.016). Vertical lines indicate the SE of the mean number of percentage of predation.

Fig. 5. Mean (±SE) percentage of cannibalism and predation in *Spalgis epius* (Se) and *Cryptolaemus montrouzieri* (Cm) in the absence of prey. Bars with different letters indicate the significant difference in percentage of predation/cannibalism (Mann–Whitney *U* test αB *P*<0.008). Vertical lines indicate the SE of the mean number of percentage of predation.

of population growth operating through a negative density-dependent feedback. IGP is generally considered as an important mechanism underlying the success of biological control (Grez *et al.*, 2012). Asymmetrical IGP in favour of *C. montrouzieri* larvae in the absence of prey could be due to the sluggish nature of *S. epius* larvae, which are more prone to interspecific attack. Larvae of *S. epius* mimic a mealybug colony by placing the mealybug debris on their back (Dinesh *et al.*, 2010) and thus escape from the attack of mealybug attendant ants (Venkatesha *et al.*, 2004). However, in the absence of mealybugs, exposed larvae of *S. epius* may be prone to interspecific attack by *C. montrouzieri* larvae. Similarly, the coccinellid aphid predator *Harmonia axyridis* (Pallas) feeds on lepidopterous larvae in the absence of its prey (Kim *et al.*, 1968; Shu & Yu, 1985; Hoogendoorn & Heimpel, 2003; Koch *et al.*, 2003). In the absence of prey, predation between *C. montrouzieri* and *S. epius* is similar to that reported among predatory coccinellids under scarce prey density (Hironori & Katsuhiro, 1997; Schellhorn & Andow, 1999; Musser & Shelton, 2003).

Maximum cannibalism by the third instar larva of *S. epius* could be due to their voracious feeding habit, which consumes a large quantity of prey compared to other larval stages (Dinesh & Venkatesha, 2011*a*, *b*). Among younger and older conspecific larval interactions, the third instar larva of *S. epius* was more cannibalistic as it attacked both the smaller second instar and the sluggish fourth instar larva. Conspecific predation in Lepidoptera with a moderate food supply or
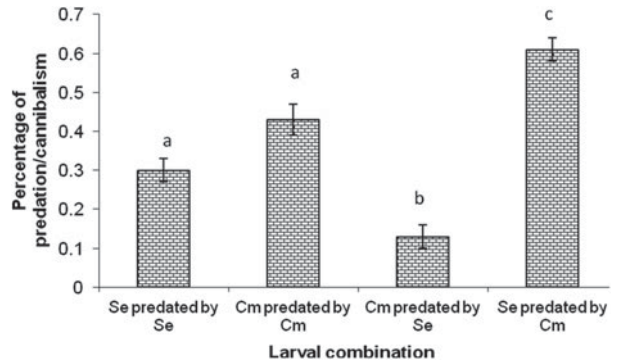
no food is common and the smallest, less healthy or less active larvae are usually attacked by more robust individuals (Dethier, 1937).

All larval instars of *C. montrouzieri* potentially predated on all larval instars of *S. epius* in the absence of prey. The relative aggressive behaviour of hungry larvae of *C. montrouzieri* towards *S. epius* may be because of their active movement compared to *S. epius* larvae. A greater cannibalistic nature of older larval instars of *C. montrouzieri* on first instar larva may be due to their differences in their body size. Moreover, the incidence of conspecific and heterospecific predation is greater when an attacker is one instar older and thus, bigger in size than its victim (Omkar *et al.*, 2005). As well, in most of ladybird species older larvae move faster than young larvae (Ng, 1988), thus fast moving older larval instars of *C. montrouzieri* easily attack and consume younger larval instars. Moreover, the bioconversion efficiency of older larval instars in predatory coccinellids is less than that of younger larvae, which suggests that older larvae feed more and convert less prey biomass into predator biomass because of high metabolic cost (Baumgartner *et al.*, 1987). Hence, requirement of more food intake in older larval instars of *C. montrouzieri* may drive them to increasingly indulge in cannibalism as well as IGP.

Absence of interspecific predation of eggs of *C. montrouzieri* by *S. epius* may be because coccinellid eggs are protected from defensive alkaloids such as pyrazines and quinolones (Agarwala & Yasuda, 2001). Hence, eggs of coccinellids are less attacked by predator species compared to eggs of pest species even in the same habitat (Cottrell & Yeargan, 1998). In contrast, some species of coccinellids feed on eggs of other coccinellids (Cottrell, 2005). However, in *C. montrouzieri* conspecific and interspecific egg predation is absent. Predation by adults of *C. montrouzieri* on all larval stages, prepupa, and pupa of *S. epius* may be due to the sluggish nature of *S. epius* larvae; and prepupa and newly formed pupa are more prone to attack as they clear prey debris present on their back during the formation of prepupa.

All in all our study provides an insight into the possible complex inter- and intraspecific predatory phenomena occurring in *S. epius* and *C. montrouzieri* in the field. In the presence of prey, the absence of cannibalism and IGP in these two

species suggests that they can be employed together in biological control when a prey population is abundant. *C. montrouzieri* larvae may serve as an additive along with voracious *S. epius* larvae in the control of mealybugs. Both *S. epius* and *C. montrouzieri* can maintain a stable coexistence in abundant prey populations and at the time of prey scarcity and at patchy prey habitats they may possess asymmetric IGP. Thus, *C. montrouzieri* may dominate the guild and becomes a threat to larvae of *S. epius* under the situation of total absence of prey. This first information is helpful to use these two predator species in the biological control of mealybugs.

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