

# Risks associated with tandem release of large and small ladybirds (Coleoptera: Coccinellidae) in heterospecific aphidophagous guilds

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**Abstract**—Multiple interactions occurring within aphidophagous guilds determine their final predation outcomes, *i.e.*, antagonistic, additive, or synergistic. Based on these predatory outcomes, the suitability of guilds in suppressing aphid pests is determined. The present study assesses the efficacy of 11 guilds, formed from both larval and adult stages of four locally abundant aphidophagous coccinellids (Coleoptera: Coccinellidae), while exploiting the pea aphid, *Acyrtosiphon pisum* Harris (Hemiptera: Aphididae). The observed antagonistic effects within these guilds are resultants of enhanced predator–predator interactions due to the size and diversity of guild predators. Smaller ladybird predators maintained their usual body mass, probably by increasing their conversion efficiencies to compensate for their reduced prey consumption. However, larger ladybirds reported loss in their body mass, owing to their higher energy needs. The overall guild conversion efficiencies and growth rates were reduced. Among the experimental guilds, the observed prey mortalities were relatively higher in two-predator guilds, and within these two-predator combinations, the higher prey mortalities were recorded in those guilds where *Coccinella septempunctata* was one of the predators.

**Résumé**—Les interactions multiples qui se produisent au sein des guildes d'aphidophages déterminent les résultats finaux de la prédation, par ex. antagonistes, additifs ou synergiques. Nous déterminons l'aptitude des guildes à éliminer les pucerons ravageurs d'après ces résultats de la prédation. Notre étude évalue l'efficacité de 11 guildes formées à la fois de stades larvaires et adultes de quatre coccinellidés (Coleoptera: Coccinellidae) aphidophages localement abondants qui exploitent le puceron du pois, *Acyrtosiphon pisum* Harris (Hemiptera: Aphididae). Les effets antagonistes observés au sein de ces guildes résultent d'interactions plus importantes entre prédateurs reliées à la taille et la diversité des guildes de prédateurs. Les coccinelles prédatrices de plus petite taille maintiennent leur masse corporelle habituelle, probablement en augmentant leurs rendements de conversion afin de compenser leur consommation réduite de proies. Cependant, les coccinelles plus grandes affichent une perte de masse corporelle à cause de leurs besoins énergétiques accrus. Les rendements de conversion globaux et les taux de croissance des guildes sont réduits. Parmi les guildes expérimentales, les mortalités observées chez les proies sont relativement plus élevées dans les guildes à deux prédateurs, et parmi ces guildes à deux prédateurs, les mortalités de proies plus élevées s'observent dans les guildes dont l'un des prédateurs est *Coccinella septempunctata*.

## Introduction

Guilds occur across different ecosystems and are formed by groups of species that together exploit a common, potentially limited resource (extra guild prey) and show interactions, ranging from cooperation and mutualism to competition

and predation. Such complex interactions between different species have been previously reported in a number of aphidophagous guilds (Evans 1991; Dixon 2000; Omkar *et al.* 2002; Zannou *et al.* 2005; Meszaros *et al.* 2007; Ware and Majerus 2008; Sato *et al.* 2009; Omkar and Pervez 2011). Ferguson and Stiling (1996) have

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reported that the interactions between guild members on being released in the field on a common aphid prey, may lead to any of the five situations: (1) they may cause higher mortality to the aphid prey than expected (synergistic interaction, Losey and Denno 1998, 1999), a phenomenon termed as “Predator Facilitation” (Charnov *et al.* 1976), (2) both the observed and expected (sum of individual prey mortalities) aphid prey mortalities are equivalent (additive interaction, Chang 1996; Straub and Snyder 2006), (3) observed aphid prey mortality may be less than the expected prey mortality, (4) observed prey mortality may be less than that caused by one predator alone but not the other, and (5) the observed prey mortality may be less than when either predators acts alone; the last three cases being antagonistic interactions (Prasad and Snyder 2004; Kajita *et al.* 2006; Majerus *et al.* 2006; Hodek and Michaud 2008).

Additive or synergistic interactions occur when the activity of one predator increases the susceptibility of a shared prey to another predator(s) (Losey and Denno 1998, 1999). However, the nonadditive or antagonistic interactions are mediated either through (i) exploitative competition where a predator reduces the abundance of a shared prey affecting the other predator(s) or (ii) through interference competition where the activity of one predator reduces the access of other predator(s) to the shared prey (Mills 2006). The consequences of such interactions among guild predators are important for the biocontrol of economically important pests. It is because of these variations in the predatory guilds that Godfray and Waage (1991) have suggested that unlicensed release of natural predators should not be encouraged and prior evaluation of combinations of natural predators for the identification of effective biocontrol agents is essential.

Among the number of factors on which the interactions within guilds are assessed, body size (biomass) of constituent predators is a crucial one that influences success or failure in the guild (Lucas *et al.* 1998; Felix and Soares 2004; Armsby and Tisch 2006; Mochizuki *et al.* 2006). Larger species have a competitive advantage over smaller species during interference competition, where owing to their large size and higher consumption rates (Finlayson *et al.* 2010),

they physically interfere with their competitors and/or prey upon them (Lawton and Hassell 1981; Persson 1985; Spiller 1986; Wissinger and McGrady 1993; Sato *et al.* 2008). In prey abundant conditions of aphidophagous guilds, larger ladybirds are more effective than the smaller ladybirds but not so under prey scarce conditions (Sloggett 2008). Prey scarce conditions are, however, better exploited by smaller ladybirds (Dixon 2007). Aphid colonies are often first attacked by a small and then a large species of ladybird, and hence the smaller species starts exploiting the resources before the larger species (Dixon 2007; Sloggett 2008), indicating them to be more effective during exploitative competition.

While exploring these interactions, earlier studies were restricted to the final guild predation outcomes (additive or nonadditive), and have not evaluated changes in guild conversion efficiencies or guild growth rates, or the body mass change of the guild predators sharing the common prey. Some recent studies revealed that larger ladybirds are more voracious and smaller ones are more efficient at prey use and suggest the use of their combinations in the form of heterospecific guilds for biocontrol purposes (Mishra *et al.* 2011, 2012). Omkar and Pervez (2011) reported synergistic functional response when *Coccinella transversalis* (Fabricius) (large ladybird) and *Propylea dissecta* (Mulsant) (small ladybird), were released in tandem.

In the present investigation, the efficacy of size-based 11 heterospecific guilds, formed from the combinations of four locally co-occurring predatory ladybirds (Coleoptera: Coccinellidae), as follows *Coccinella septempunctata* (Linnaeus), *C. transversalis*, *Cheilomenes sexmaculata* (Fabricius), and *P. dissecta* on the pea aphid, *Acyrtosiphon pisum* (Harris) (Hemiptera: Aphididae) have been assessed. Of the four ladybirds, the former two are large and the later two are small ones (Mishra *et al.* 2011). The aphid prey forms an equivalent niche for these locally abundant aphidophagous ladybirds that coexist as its predators (Mishra *et al.* 2011).

The inefficiencies of additive models have enforced us to use multiplicative risk model (Soluk and Collins 1988; Sih *et al.* 1998) in the present study to analyse the “additive” or “nonadditive” effects. Additive models normally

generate higher or unrealistic “expected prey mortality” and cannot correct for prey depletion within additive experimental designs, and in such cases “multiplicative risk model” is a more appropriate null model for the prey response variables that are usually measured (*e.g.*, proportion or number of prey killed or surviving; see Sih *et al.* 1998; Mills 2006).

The present investigation, therefore, aims to assess (i) size-based predatory interactions (synergistic/additive/antagonistic) within hetero-specific guilds, (ii) costs of being large while sharing common aphid prey, in view of the adaptive significance of being large (as eliminating competitors) but its negative aspects are poorly understood (Sato *et al.* 2008), (iii) changes within guild conversion efficiencies and guild growth rates, and (iv) finding the suitable hetero-specific guild(s) for biocontrol purposes.

## Materials and methods

### Stock maintenance

Adults of four predaceous ladybird species, as follows *C. septempunctata* (C7), *C. transversalis* (Ct), *C. sexmaculata* (Cs), and *P. dissecta* (Pd) were collected from agricultural fields around the city of Lucknow, India (26°50'N, 80°54'E), placed in plastic Petri dishes (14.5 × 1.5 cm) and reared under constant abiotic conditions (27 ± 1 °C; 65 ± 5% relative humidity; 14:10 hours light:darkness) in Environmental Test Chambers (ETC, CH-6S, Remi Instruments, India). Adults were fed with *ad libitum* supply of aphid, *A. pisum* on broad bean, *Vicia faba* Linnaeus (Fabaceae) maintained in polyhouse (22 ± 1 °C; 65 ± 5% relative humidity and 14 hours light:10 hours dark photoperiod). Eggs laid were collected every 24 hours and observed for hatching. The newly hatched larvae were isolated and reared till adult emergence in separate Petri dishes with a daily-replenished supply of aphids. Being the most voracious predatory stages, fourth instar larvae (12 hours after moulting) and 10-day-old unmated adult females were used in the experiments. Unmated adult females were used to avoid error due to exceptionally high variations in the reproductive potential of these ladybird species (Omkar 2004; Omkar *et al.* 2005).

### Experimental design

Prior to experimentation, the fourth instar of the predatory species was starved for 12 hours. At the start of the experiment, the larvae were massed using an electronic balance (Sartorius CP225-D; Sartorius AG, Goettingen, Germany; 0.01 mg precision). A single pre-massed fourth instar was kept in a plastic Petri dish (14.5 × 1.5 cm) along with 50 mg of aphid at constant abiotic conditions (27 ± 1 °C; 65 ± 5% relative humidity; 14:10 hours light:darkness) in ETC for 24 hours. The larva was then separated from the aphid biomass and both were massed individually. This was repeated 10 times. Similar experiments were also carried out for the remaining predatory species (*n* = 40). The reduction in aphid biomass in presence of predator(s) was considered to be due to prey mortality.

To evaluate the combined predatory potential of ladybird species, guilds were formed on the basis of the size of the ladybird predators (segregated according to mean body mass of predators; C7 = 17.7 ± 1.99<sup>b</sup> mg; Ct = 15.3 ± 0.90<sup>b</sup> mg; Cs = 8.8 ± 0.91<sup>a</sup> mg; and Pd = 7.2 ± 0.81<sup>a</sup> mg; *F* = 16.25; *P* < 0.0001; *df* = 3, 39, based on one-way ANOVA followed by Tukey's *post hoc* comparison of means and superscript “a” and “b” mean statistically significant differences). These were S + S (Cs + Pd), L + S (C7 + Cs, C7 + Pd, Ct + Cs, Ct + Pd), L + L (C7 + Ct), 2L + S (C7 + Ct + Pd, C7 + Ct + Cs), L + 2S (C7 + Cs + Pd, Ct + Cs + Pd), and 2L + 2S (C7 + Ct + Cs + Pd) (L = large; S = small). Within these guilds, combinations of two, three, and four heterospecific fourth instar were placed in plastic Petri dishes (14.5 × 1.5 cm) having one individual of each predatory species along with aphid mass equivalent to 100 mg (for two predators), 150 mg (for three predators), and 200 mg (for four predators) of *A. pisum*, and maintained at the above mentioned standard abiotic conditions for 24 hours. Prior to experimentation, the relative prey–predator proportion was standardised and this proportion remained unaltered to prevent intraguild predation. Also, the size of experimental arena was kept constant to promote the maximum possible predatory interactions between the guild species. The larvae were massed individually prior and post experiment. Each treatment was replicated 10 times.

Similar experiments were also repeated with heterospecific unmated 10-day-old adult females ( $C7 = 27.8 \pm 1.32^c$  mg;  $Ct = 21.3 \pm 1.32^b$  mg;  $Cs = 14.4 \pm 1.61^a$  mg; and  $Pd = 11.5 \pm 0.50^a$  mg;  $F = 33.43$ ;  $P < 0.0001$ ;  $df = 3, 39$ ), individually ( $n = 40$ ) and within combinations ( $n = 110$ ). During the selection of aphid size, intermediate instars of *A. pisum* were taken to allow best development and survival for both larger and smaller ladybird predators (Roger *et al.* 2000).

To assess the natural reduction in aphid biomass, if any, in the absence of predators, all four standard biomass, as follows 50, 100, 150, and 200 mg of aphids, were placed in Petri dishes and kept under similar conditions for 24 hours, remassed and considered as controls. The average loss of biomass, if any, based on five replicates per standard aphid biomass, was used to normalise the data on consumption prior to calculating the various parameters (Tables 1 and 2).

**Statistical analysis**

We aimed to decipher through statistical analysis of data (1) size-based predatory interactions within guilds while sharing common aphid prey, (2) the changes in guild conversion efficiencies, guild growth rates, and individual predator biomass within each guild. All data obtained in the study were checked for normal distribution using Kolmogorov–Smirnov test for normality and Bartlett’s test for homogeneity of variances prior to being subjected to further analysis.

**Multiplicative risk model and predatory interactions**

The expected/observed aphid prey mortality within 24 hours by each guild combination was assessed by “multiplicative risk model” (using equations (1), (2), (3), and (4)), to correct for prey depletion within additive experimental designs (see Soluk and Collins 1988; Sih *et al.* 1998).

1. Proportion of aphid prey mortality by predator A or B or C or D alone (Pa or Pb or Pc or Pd)

$$= \frac{\text{Aphid prey mortality (mg) by predator A or B or C or D alone}}{\text{Aphid prey (mg) provided to predator A or B or C or D alone}}$$

(For larval guilds,  $Pa (C7) = 0.65 \pm 0.04$ ;  $Pb (Ct) = 0.61 \pm 0.06$ ;  $Pc (Cs) = 0.53 \pm 0.07$ ;  $Pd (Pd) = 0.50 \pm 0.08$ );

(For adult guilds,  $Pa (C7) = 0.89 \pm 0.04$ ;  $Pb (Ct) = 0.70 \pm 0.04$ ;  $Pc (Cs) = 0.68 \pm 0.03$ ;  $Pd (Pd) = 0.48 \pm 0.03$ )

2. Expected proportion of aphid prey mortality

$$= 1 - [(1 - Pa)(1 - Pb)]_{Two};$$

$$1 - [(1 - Pa)(1 - Pb)(1 - Pc)]_{Three};$$

$$1 - [(1 - Pa)(1 - Pb)(1 - Pc)(1 - Pd)]_{Four};$$

where Pa, Pb, Pc, and Pd are proportion of aphid prey mortality by predator A, B, C, and D alone, respectively.

3. Observed proportion of aphid prey mortality (within guild)

$$= \frac{\text{Combined aphid prey mortality (mg) (by two or three or four predator species)}}{\text{Aphid prey provided (mg)}}$$

4. Expected/observed aphid prey mortality (%)

$$= \text{expected/observed proportion of aphid prey mortality} \times 100$$

Variation in expected and observed aphid prey mortality within each guild was analysed using one-way ANOVA. Before to ANOVA, all per cent data were subjected to arcsine square root transformation.

For assessing the influence of guild size (or predator diversity) on predatory interactions, the data were subjected to two-way ANCOVA (general linear model) with predatory stage (larval and adult) and guild size (S + S, L + S, L + L, 2L + S, L + 2S, and 2L + 2S) as independent factors, observed prey mortality as dependent factor and guild biomass (combined biomass of the predator species constituting that guild) as a covariate (general linear model) followed by Tukey’s post hoc comparison of means.

Further, for assessing the effect of increasing guild size (predator diversity) on observed prey mortality, the data were subjected to Pearson’s correlation analysis.

**Conversion efficiencies, growth rates and individual predator biomass within each guild**

The conversion efficiencies and growth rates within each guild (fourth instar and

**Table 1.** Observed and expected prey mortalities (%) showing overall predatory interactions using multiplicative risk model in fourth instar guilds.

Guild size	Guild predators	Combined prey mortality (mg)	Sum of individual prey mortalities (mg)	Multiplicative risk model (fourth instar)			Predatory interaction
				Observed prey mortality (%)	Expected prey mortality (%)	<i>F</i> -value ( <i>P</i> -value)	
L + L	C7 + Ct	68.4 ± 3.8	63.0 ± 3.3	68.4 ± 3.8 <sup>c</sup>	86.9 ± 2.5	16.60 (0.001)	Antagonism
L + S	C7 + Cs	64.9 ± 4.9	58.9 ± 3.7	64.9 ± 4.9 <sup>cde</sup>	83.7 ± 2.8	10.88 (0.004)	Antagonism
	C7 + Pd	66.1 ± 5.5	57.6 ± 4.6	66.1 ± 5.5 <sup>de</sup>	82.1 ± 3.7	5.85 (0.026)	Antagonism
	Ct + Cs	58.9 ± 4.3	56.9 ± 4.9	58.9 ± 4.3 <sup>bcde</sup>	81.2 ± 5.4	10.61 (0.004)	Antagonism
	Ct + Pd	40.1 ± 6.0	55.6 ± 5.4	40.1 ± 6.0 <sup>ab</sup>	79.9 ± 4.4	28.91 (<0.0001)	Antagonism
	Cs + Pd	58.8 ± 2.9	51.5 ± 4.6	58.8 ± 2.9 <sup>bcde</sup>	77.6 ± 5.0	10.50 (0.005)	Antagonism
L + L + S	C7 + Ct + Cs	48.9 ± 4.9	89.4 ± 4.9	32.6 ± 5.1 <sup>a</sup>	93.6 ± 2.1	122.08 (<0.0001)	Antagonism
	C7 + Ct + Pd	66.1 ± 7.6	88.1 ± 5.7	44.1 ± 5.1 <sup>abc</sup>	93.1 ± 0.0	84.86 (<0.0001)	Antagonism
L + S + S	C7 + Cs + Pd	63.0 ± 7.4	84.0 ± 5.1	42.0 ± 4.9 <sup>bc</sup>	92.1 ± 0.0	90.39 (<0.0001)	Antagonism
	Ct + Cs + Pd	67.2 ± 6.1	82.0 ± 6.1	44.8 ± 4.0 <sup>abcd</sup>	90.7 ± 0.0	83.45 (<0.0001)	Antagonism
L + L + S + S	C7 + Ct + Cs + Pd	71.3 ± 7.9	114.5 ± 6.3	35.6 ± 3.9 <sup>a</sup>	96.8 ± 1.1	222.65 (<0.0001)	Antagonism

Values are mean ± SE; *F*-values significant at  $P < 0.05$ ;  $df = 1, 19$ .

L, S, C7, Ct, Cs, and Pd represent large, small, *Coccinella septempunctata*, *Coccinella transversalis*, *Cheilomenes sexmaculata*, and *Propylea dissecta*, respectively.

<sup>a,b,c,d,e</sup> Lowercase letters represent comparison of means within guild predators based on Tukey's *post hoc* comparison of means.

**Table 2.** Observed and expected prey mortalities (%) showing overall predatory interactions using multiplicative risk model in adult female guilds.

Guild size	Guild predators	Combined prey mortality (mg)	Sum of individual prey mortalities (mg)	Multiplicative risk model (adult females)			Predatory interaction
				Observed prey mortality (%)	Expected prey mortality (%)	<i>F</i> -value ( <i>P</i> -value); df	
L + L	C7 + Ct	68.4 ± 3.8	79.9 ± 2.0	68.4 ± 3.8 <sup>cd</sup>	97.7 ± 0.4	59.74 (<0.0001)	Antagonism
L + S	C7 + Cs	76.3 ± 6.5	78.5 ± 2.0	76.3 ± 6.5 <sup>d</sup>	97.1 ± 0.8	9.99 (0.005)	Antagonism
	C7 + Pd	68.3 ± 7.1	68.9 ± 2.5	68.3 ± 7.1 <sup>cd</sup>	94.4 ± 2.2	12.30 (0.003)	Antagonism
	Ct + Cs	58.6 ± 3.7	69.0 ± 2.6	58.6 ± 3.7 <sup>bcd</sup>	90.5 ± 1.8	59.51 (<0.0001)	Antagonism
	Ct + Pd	56.6 ± 2.3	59.4 ± 2.9	56.6 ± 2.3 <sup>bcd</sup>	84.4 ± 2.6	64.76 (<0.0001)	Antagonism
	Cs + Pd	53.7 ± 2.0	58.0 ± 2.0	53.7 ± 2.0 <sup>abc</sup>	83.4 ± 2.0	110.87 (<0.0001)	Antagonism
L + L + S	C7 + Ct + Cs	113.6 ± 5.3	113.7 ± 1.9	32.6 ± 5.1 <sup>a</sup>	99.3 ± 0.1	171.23 (<0.0001)	Antagonism
	C7 + Ct + Pd	112.3 ± 7.2	104.1 ± 2.9	44.1 ± 5.1 <sup>ab</sup>	98.8 ± 0.2	115.28 (<0.0001)	Antagonism
L + S + S	C7 + Cs + Pd	66.0 ± 2.3	102.7 ± 2.4	42.0 ± 4.9 <sup>ab</sup>	98.5 ± 0.5	131.08 (<0.0001)	Antagonism
	Ct + Cs + Pd	73.5 ± 3.3	93.2 ± 3.2	44.8 ± 4.0 <sup>ab</sup>	94.9 ± 1.1	142.32 (<0.0001)	Antagonism
L + L + S + S	C7 + Ct + Cs + Pd	141.0 ± 8.2	137.9 ± 2.7	70.5 ± 4.1 <sup>cd</sup>	99.6 ± 0.0	50.74 (<0.0001)	Antagonism

Values are mean ± SE; *F*-values significant at  $P < 0.05$ ; df = 1, 19.

L, S, C7, Ct, Cs, and Pd represent Large, Small, *Coccinella septempunctata*, *Coccinella transversalis*, *Cheilomenes sexmaculata*, and *Propylea dissecta*, respectively.

<sup>a,b,c,d</sup> Lowercase letters represent comparison of means within guild predators based on Tukey's *post hoc* comparison of means.

**Table 3.** Conversion efficiencies in heterospecific fourth instar and adult female guilds.

Guild predators	Fourth instar guilds				Adult female guilds			
	Conversion efficiency				Conversion efficiency			
	Combined prey mortality	Sum of individual prey mortality	Combined prey mortality versus individual prey mortality	Effects	Combined prey mortality	Sum of individual prey mortality	Combined prey mortality versus individual prey mortality	Effects
(C7 + Ct)	0.210 ± 0.016	0.272 ± 0.019	$F = 6.61; P = 0.019$	(↓)	0.093 ± 0.055	0.203 ± 0.005	$F = 19.51; P < 0.0001$	(↓)
(C7 + Cs)	0.149 ± 0.019	0.221 ± 0.019	$F = 7.60; P = 0.013$	(↓)	0.065 ± 0.028	0.104 ± 0.007	$F = 7.02; P = 0.016$	(↓)
(C7 + Pd)	0.139 ± 0.027	0.226 ± 0.027	$F = 9.44; P = 0.007$	(↓)	0.082 ± 0.007	0.140 ± 0.033	$F = 5.28; P = 0.034$	(↓)
(Ct + Cs)	0.130 ± 0.020	0.210 ± 0.016	$F = 11.12; P = 0.004$	(↓)	0.069 ± 0.019	0.158 ± 0.013	$F = 13.59; P = 0.002$	(↓)
(Ct + Pd)	0.125 ± 0.021	0.202 ± 0.021	$F = 6.70; P = 0.019$	(↓)	0.060 ± 0.018	0.140 ± 0.012	$F = 13.24; P = 0.002$	(↓)
(Cs + Pd)	0.030 ± 0.016	0.061 ± 0.009	$F = 51.45; P < 0.0001$	(↓)	0.058 ± 0.018	0.139 ± 0.014	$F = 24.55; P < 0.0001$	(↓)
(C7 + Ct + Cs)	0.137 ± 0.037	0.229 ± 0.015	$F = 17.92; P < 0.0001$	(↓)	0.060 ± 0.024	0.127 ± 0.007	$F = 29.68; P < 0.0001$	(↓)
(C7 + Ct + Pd)	0.153 ± 0.020	0.210 ± 0.015	$F = 9.04; P = 0.008$	(↓)	0.030 ± 0.022	0.100 ± 0.005	$F = 6.79; P = 0.018$	(↓)
(C7 + Cs + Pd)	0.100 ± 0.039	0.200 ± 0.015	$F = 5.76; P = 0.027$	(↓)	0.046 ± 0.008	0.090 ± 0.007	$F = 17.02; P = 0.001$	(↓)
(Ct + Cs + Pd)	0.100 ± 0.019	0.200 ± 0.018	$F = 14.46; P = 0.001$	(↓)	0.067 ± 0.010	0.175 ± 0.017	$F = 26.74; P < 0.0001$	(↓)
(C7 + Ct + Cs + Pd)	0.055 ± 0.020	0.210 ± 0.012	$F = 75.47; P < 0.0001$	(↓)	0.037 ± 0.020	0.090 ± 0.006	$F = 30.81; P < 0.0001$	(↓)

Values are mean ± SE;  $F$ -values significant at  $P < 0.05$ ;  $df = 1, 19$ .

C7, Ct, Cs, and Pd represent *Coccinella septempunctata*, *Coccinella transversalis*, *Cheilomenes sexmaculata*, and *Propylea dissecta*, respectively.

(↑), (→), and (↓) represent gain, no change, or loss in conversion efficiencies, respectively, based on Tukey's *post hoc* comparison of means.

**Table 4.** Growth rates in heterospecific fourth instar and adult female guilds.

Guild predators	Fourth instar guilds				Adult female guilds			
	Growth rate (mg/day)				Growth rate (mg/day)			
	Combined prey mortality	Sum of individual prey mortality	Combined prey mortality versus individual prey mortality	Effects	Combined prey mortality	Sum of individual prey mortality	Combined prey mortality versus individual prey mortality	Effects
(C7 + Ct)	0.44 ± 0.04	0.65 ± 0.04	$F = 11.22; P = 0.004$	(↓)	0.15 ± 0.04	0.26 ± 0.01	$F = 37.22; P < 0.0001$	(↓)
(C7 + Cs)	0.26 ± 0.09	0.53 ± 0.06	$F = 13.36; P = 0.002$	(↓)	0.14 ± 0.03	0.24 ± 0.01	$F = 23.32; P < 0.0001$	(↓)
(C7 + Pd)	0.29 ± 0.08	0.48 ± 0.07	$F = 19.53; P < 0.0001$	(↓)	0.12 ± 0.04	0.25 ± 0.01	$F = 48.17; P < 0.0001$	(↓)
(Ct + Cs)	0.27 ± 0.08	0.51 ± 0.15	$F = 20.18; P < 0.0001$	(↓)	0.16 ± 0.02	0.24 ± 0.02	$F = 9.29; P = 0.007$	(↓)
(Ct + Pd)	0.25 ± 0.09	0.49 ± 0.06	$F = 30.55; P < 0.0001$	(↓)	0.10 ± 0.03	0.26 ± 0.03	$F = 11.27; P = 0.004$	(↓)
(Cs + Pd)	0.14 ± 0.07	0.61 ± 0.05	$F = 26.88; P < 0.0001$	(↓)	0.13 ± 0.04	0.27 ± 0.03	$F = 10.08; P = 0.005$	(↓)
(C7 + Ct + Cs)	0.18 ± 0.08	0.48 ± 0.04	$F = 11.67; P = 0.003$	(↓)	0.07 ± 0.03	0.20 ± 0.01	$F = 45.50; P < 0.0001$	(↓)
(C7 + Ct + Pd)	0.20 ± 0.07	0.47 ± 0.05	$F = 25.33; P < 0.0001$	(↓)	0.09 ± 0.04	0.16 ± 0.03	$F = 15.87; P = 0.001$	(↓)
(C7 + Cs + Pd)	0.25 ± 0.10	0.51 ± 0.06	$F = 4.99; P = 0.038$	(↓)	0.09 ± 0.04	0.17 ± 0.01	$F = 30.80; P < 0.0001$	(↓)
(Ct + Cs + Pd)	0.20 ± 0.08	0.50 ± 0.04	$F = 56.44; P < 0.0001$	(↓)	0.10 ± 0.05	0.18 ± 0.02	$F = 14.44; P < 0.0001$	(↓)
(C7 + Ct + Cs + Pd)	0.07 ± 0.05	0.49 ± 0.03	$F = 42.52; P < 0.0001$	(↓)	0.07 ± 0.04	0.17 ± 0.01	$F = 5.13; P = 0.036$	(↓)

Values are mean ± SE;  $F$ -values significant at  $P < 0.05$ ;  $df = 1, 19$ .

C7, Ct, Cs and Pd represent *Coccinella septempunctata*, *Coccinella transversalis*, *Cheilomenes sexmaculata*, and *Propylea dissecta*, respectively.

(↑), (→) and (↓) represent gain, no change, or loss in growth rates, respectively, based on Tukey's *post hoc* comparison of means.



adult females) were calculated using following formulae:

1. Conversion efficiency (modified after Dixon 2000)

$$= \frac{\text{Change in guild biomass (mg)}}{\text{Biomass of prey consumed within the guild (mg)}}$$

2. Growth rate ( $\text{day}^{-1}$ ) (modified after Waldbauer 1968; Ramdev and Rao 1979)

$$= \frac{\text{Change in guild biomass (mg)}}{\text{Duration of feeding period (days)} \times \text{Mean guild biomass (mg)}}$$

Variations in conversion efficiencies, growth rates and biomass change of predators within guilds and when placed individually were analysed using one way ANOVA, followed by Tukey's post hoc comparison of means.

All statistical analyses were performed using MINITAB 16 (Minitab Inc., State College, Pennsylvania, United States of America).

## Results

### Multiplicative risk model and predatory interactions

Statistical tests revealed that both larval and adult guilds revealed antagonistic effects, *i.e.* within each guild, observed prey mortality was less than the expected prey mortality (Tables 1 and 2).

Results of two-way ANCOVA further revealed that within both larval and adult guilds, the observed prey mortality was influenced by the guild size ( $F_{\text{ANCOVA (stage} \times \text{guild size)}} = 4.22$ ;  $P = 0.001$ ;  $df = 5, 219$ ). Also, within the guilds of similar size, guild biomass ( $F_{\text{ANCOVA (covariate)}} = 16.60$ ;  $P < 0.0001$ ;  $df = 1, 219$ ) significantly affected the observed prey mortality.

Further, observed prey mortality was found to have an inverse linear relationship with the guild size in both larval ( $r = -0.507$ ,  $P < 0.0001$ ) and adult ( $r = -0.759$ ,  $P < 0.0001$ ) guilds. With increasing guild size or the predator richness, reduction in aphid prey mortality was observed. Larval guild of C7 + Ct and C7 + Cs adult guild resulted in maximum prey mortality.

### Conversion efficiencies, growth rates and individual predator biomass within each guild

Results of one-way ANOVA revealed lower conversion efficiencies (Table 3) and growth rates (Table 4) within larval and adult guilds while sharing common aphid prey.

Within larval and adult guilds the larger ladybirds (*C. septempunctata* and *C. transversalis*) reported decline whereas the smaller ladybirds (*C. sexmaculata* and *P. dissecta*) reported no changes in their body mass (Figs 1, 2).

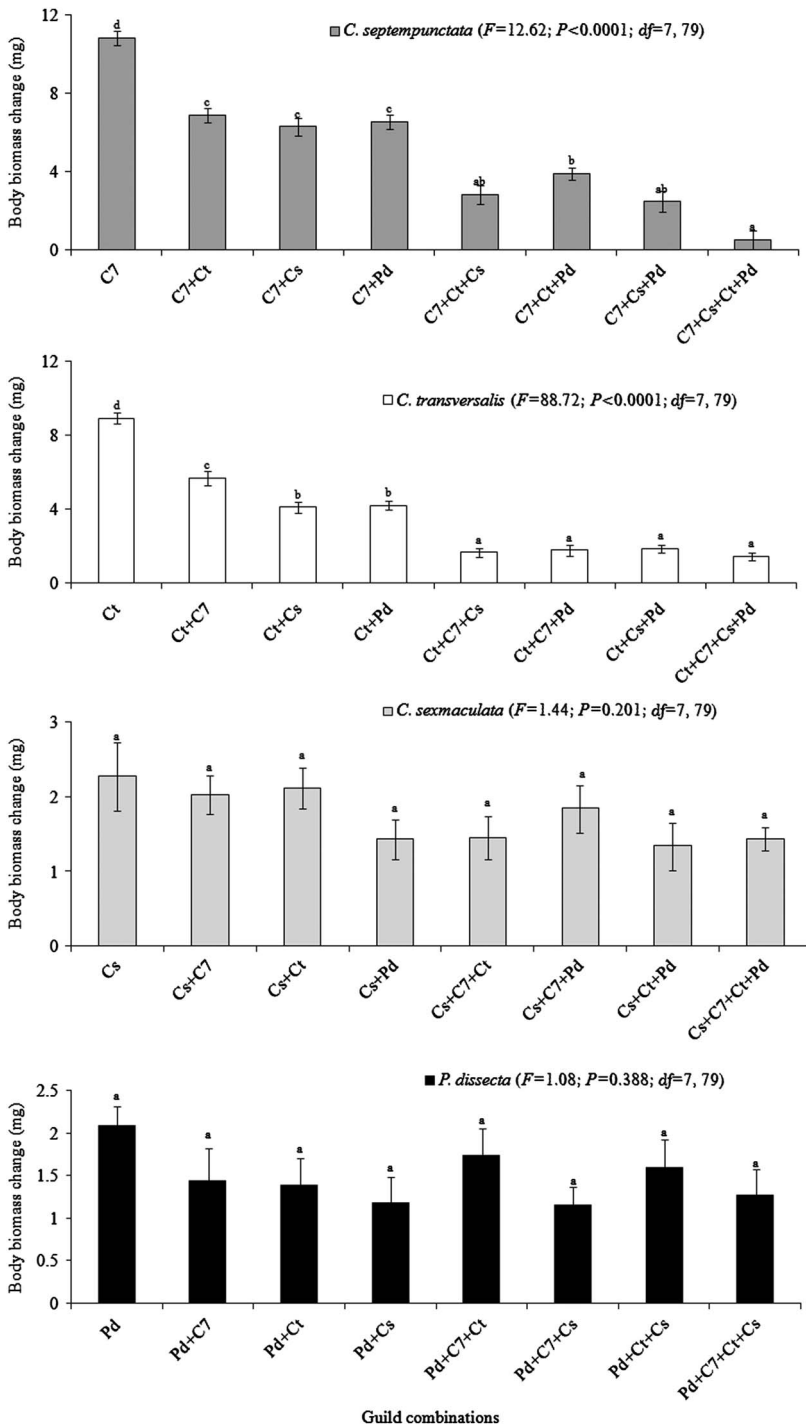
## Discussion

In the present study, both the larval and adult guilds with multiple predators have shown antagonistic effects. Decreased aphid prey mortality with increase in predator richness within the guild probably indicates the existence of predator–predator interactions, either through interference competition and/or the exploitative competition (Michelakis 1973; Hassell *et al.* 1976; Eveleigh and Chant 1982). In the presence of multiple predators, it is believed that the area searched by individual predators decreases (Pandey *et al.* 1984) and they probably consume less aphid prey than their usual predation rates (Muller and Godfray 1999; Amarasekare 2000; Noia *et al.* 2008; Hodek *et al.* 2012). Results indicating antagonistic effects on use of multiple predators have been reported in many earlier studies (Snyder and Ives 2001; Eubanks *et al.* 2002; Kaplan and Eubanks 2002; Denno and Finke 2006).

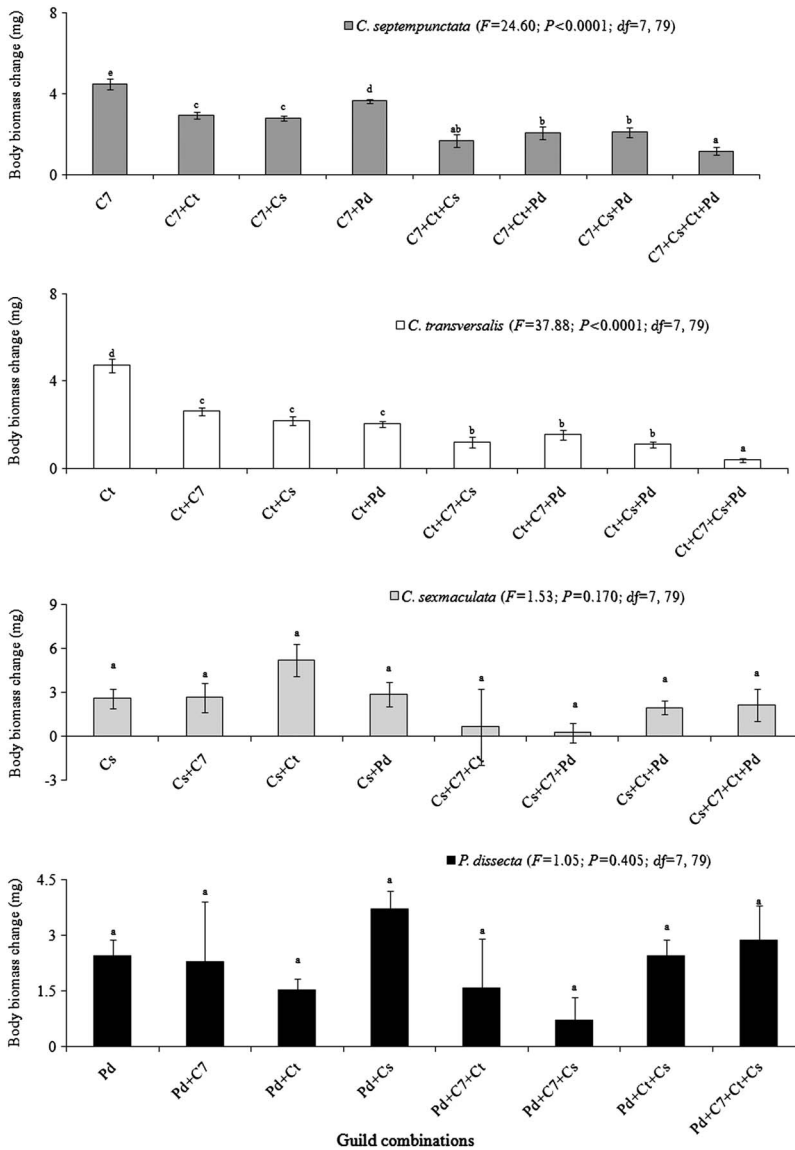
The recorded antagonistic effects and the influence of guild size and/or guild biomass on the observed prey mortality within the larval and adult guilds further reveal that the responses of ladybird predators under experimental conditions are associated with the difference in their body size.

Larger ladybirds have the capacity to feed on large aphids at both low and high densities, but need high quantity of small aphids to sustain themselves (Dixon and Hemptinne 2001; Dixon 2007; Sloggett 2008; Sloggett *et al.* 2009). Despite the presence of intermediate aphid instars in the experimental arena (equally suitable for both the large and small ladybirds) of the present study, larger ladybirds have shown reduction

**Fig. 1.** Body mass change (mg) by individual Coccinellidae while sharing the common prey population (combined predation) in fourth instar guilds. C7, Ct, Cs, and Pd represent *Coccinella septempunctata*, *Coccinella transversalis*, *Cheilomenes sexmaculata*, and *Propylea dissecta*, respectively. *F*-value significant  $P < 0.05$ .



**Fig. 2.** Body mass change (mg) by individual Coccinellidae while sharing the common prey population (combined predation) in adult female guilds. C7, Ct, Cs, and Pd represent *Coccinella septempunctata*, *Coccinella transversalis*, *Cheilomenes sexmaculata*, and *Propylea dissecta*, respectively. *F*-value significant  $P < 0.05$ .



in their usual body mass when kept with either larger or smaller ladybird predators. This might be (i) due to the consumption of less aphid prey, and/or (ii) the consumption of aphid prey less efficiently, owing to their lower conversion efficiencies and growth rates (Mishra *et al.* 2012).

On the contrary, small ladybirds are more efficient in exploiting small aphids under both low and high aphid densities due to their lower food

requirements; hence, they show a competitive advantage over larger ones during exploitative competition (Obrycki *et al.* 1998; Evans 2004). Eventually, with their reduced energy requirements and higher conversion efficiencies (Mishra *et al.* 2011, 2012), they may compensate for reduced prey consumption by further enhancing their prey exploitation and conversion efficiencies, resulting in attainment of their usual body mass, as

reported by Schuder *et al.* (2004) in the larvae of smaller ladybird, *Adalia bipunctata* (Linnaeus) under reduced prey availability.

The reduction in guild conversion efficiencies and guild growth rates also strengthens the presence of predator–predator interactions among the constituent guild predators. Studies have shown that species-specific morphological and behavioural tendencies like large body size, strong larval spines, chemical protection, rapid larval development, great nutritional plasticity, and high aggressiveness (Labrie *et al.* 2006; Pervez and Omkar 2006; Sato *et al.* 2008) play a vital role in influencing predation, and in many cases, even lead to displacement of many native predatory species (Dixon 2000; Ware and Majerus 2008; Gardiner *et al.* 2011; Grez *et al.* 2012). Also, during such interactions, species-specific toxins or alkaloids (Hautier *et al.* 2011) adversely affect the foraging behaviour of co-guild predators (Agarwala *et al.* 2003; Wilder and Rypstra 2004; Magalhães *et al.* 2005; Nakashima *et al.* 2006; Montserrat *et al.* 2007; Rypstra *et al.* 2007).

Among the experimental guilds, the observed prey mortalities were relatively higher in two-predator guilds, probably due to low predator–predator interactions. Within these two-predator combinations, the highest prey mortalities were recorded in those guilds (C7 + Ct within larval and C7 + Cs within adult guilds) where *C. septempunctata* was one of the predators. This may be due to its large size and exceptionally high voracity than the other ladybird species. These and similar other intrinsic properties of *C. septempunctata* are also associated with its dominance in most habitats of Palaearctic and Nearctic regions (Omkar and Pervez 2002; Hodek and Michaud 2008).

The results indicate that larger ladybirds have higher voracities (Finlayson *et al.* 2010; Mishra *et al.* 2011), and smaller ladybirds have higher conversion efficiencies (Mishra *et al.* 2012), and both have competitive advantages over each other during interference and exploitative competitions, respectively. Yet, the extraguild aphid prey is at lower risk of being preyed when both are released in tandem under laboratory conditions. Also, in the same field, despite exploitative or interference competitions, both these large and smaller ladybirds co-exist. This may be attributed to their tendency to feed on larger and

smaller aphid instars, respectively (Sloggett 2008), their tendency to occupy different spatial positions (Omkar and Mishra 2003; Lucas *et al.* 2004; Janssen *et al.* 2007) or they are benefitted intrinsically (Omkar *et al.* 2005; Hodek and Michaud 2008). However, to validate and strengthen the findings, laboratories and field studies are still needed.

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