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Survival, development and life tables of two congeneric ladybirds in aphidophagous guilds

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Abstract Two congeneric aphidophagous ladybirds, *Coccinella septempunctata* and *Coccinella transversalis,* were reared on three aphid species, *Lipaphis erysimi*, *Myzus persicae* and *Aphis nerii*, to estimate the effect of prey quality and intra- and interspecific interactions on their survival and development of life stages. Mortality of first instar ladybirds of both species was highest feeding on *A. nerii.* Preimaginal mortality was lowest when feeding on *L. erysimi* (*C. septempunctata,* 1.6% and *C. transversalis,* 3.2%), and highest when feeding on *A. nerii* (*C. septempunctata,* 6.2% and *C. transversalis*, 8.2%). Comparatively higher weight and larger size of *C. septempunctata* along with the lower levels of mortality recorded suggested that it is more likely to have acted as an intraguild predator than *C. transversalis*. High recorded mortality of *C. transversalis* is attributed to probable intraguild predation on account of its smaller size. The major sources of mortality were probably cannibalism, intraguild predation and other unknown factors. Lower prey quality increased the incidence of cannibalism and intraguild predation, especially in *C. transversalis*. The investigation suggests an intrinsic competitive advantage for *C. septempunctata* over *C. transversalis* in guilds of three aphid species.

Key words *Coccinella septempunctata*, *Coccinella transversalis*, ladybirds, life table, aphids, cannibalism, intraguild predation
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Introduction

Natural enemies belonging to many predatory and parasitic species converge in an aphid patch and often compete with one another for this food source (Muller & Godfray, 1999). Competition for food becomes more pronounced if the prey resource is patchy and short lived as in the case of aphids (Dixon, 1997). These intra- and interspecific competitions between predators sharing a patchy resource for their subsistence are drawing the attention of scientists (Polis *et al*., 1989; Polis & Holt, 1992; Yasuda *et al*., 2001; Agarwala *et al*., 2003). Cannibalism and intraguild predation (IGP) are the most common of these interactions. Cannibalism (e.g., Osawa, 1989; Agarwala & Dixon, 1991) and intraguild predation (IGP) - (Agarwala & Dixon, 1991; Yasuda & Ohnuma, 1999; Kajita *et al*., 2000; White & Eigenbrode, 2000; Michaud & Grant, 2003; Sato *et al*., 2003; Felix & Soares, 2004; Snyder *et al*., 2004a, b) have been extensively studied and reviewed (Polis *et al*., 1989; Polis & Holt, 1992; Omkar *et al*., 2002). These interactions in an aphidophagous guild either lead to stabilization of prey-predator populations (Godfray & Pacala, 1992) or adversely affect the foraging and oviposition performance of predators (Agarwala *et al*., 2003). Ladybirds are major components of aphidophagous guilds; their immature and adult stages are dependent on the aphid prey for their development and oviposition, respectively. Life stages of the ladybirds in the absence of the prey lead to intra- and inter-specific predation (Agarwala & Dixon, 1992; Yasuda & Katsuhiro, 1997; Agarwala *et al*., 1998; Yasuda *et al*., 2001).

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Life table studies of ladybird predators of an aphidophagous guild will help in estimating the attributes of population growth, identifying the vulnerable life stages through mathematical equations (Birch, 1948), the trends and causes of mortality (Obrycki *et al*., 1997, 1998a, b; Yasuda & Katsuhiro, 1997; Gupta, 2005). In ladybirds, life tables have been previously constructed for studying age-specific development and mortality (Mellors & Helgesen, 1980; Osawa, 1992, 1993; Kindlmann *et al*., 2000; Omkar & Pervez, 2004; Srivastava & Omkar, 2004). Despite extensive life table studies there is very little information on coccinellid life tables in two-predator systems. Among aphidophagous coccinellids, *Coccinella septempunctata* and *Coccinella transversalis* are congeneric and are the most common in India (Omkar & Bind, 1993). Of these, *C. septempunctata* is reputed to have caused decreases in indigenous coccinellid populations (Ives, 1981; Polis *et al*., 1989; Takahashi, 1989; Hemptinne *et al*., 1993; Ormord, 1994; Elliot *et al*., 1996; Phoofolo & Obrycki, 1998; Yasuda *et al*., 2001; Omkar & Pervez, 2004; Sato *et al*., 2005). Though there is some information on intraguild predation involving *C. septempunctata,* there is almost no information on *C. transversalis*. No study has quantitatively evaluated the potential interactions between these congeneric ladybirds. The objective of the present study was to estimate the survival and development and construct life table of *C. septempunctata* and *C. transversalis* because of their co-existence and thus larval interactions in a guild of three aphid species, *viz. Lipaphis erysimi* (Kaltenbach), *Myzus persicae* (Sulzer), and *Aphis nerii* Boyer de Fonsclombe. Earlier studies on influence of prey quality have reported that *L. erysimi* is the essential (high quality), *M. persicae* is the accepted (intermediate quality) and *A. nerii* was the rejected (low quality) prey of both *C. septempunctata* and *C. transversalis* (Omkar & Srivastava, 2003; Omkar & James, 2003).

Materials and methods

Insects

Adults of *C. septempunctata* and *C. transversalis* were collected from bean fields (*Dolichos lablab*) infested with *A. craccivora* in Lucknow (India). They were sexed and paired in glass beakers (10 cm × 12 cm) and fed *ad libitum A. craccivora*. Beakers were kept in environmental test chambers, maintained at 25℃ ± 2℃, 60% ± 5% RH, and 12 : 12 L : D. Eggs were laid by the females on the twigs/leaves of the host plants inside the beakers. The eggs were collected from the twigs and were kept separately in other Petri dishes. Eggs and newly hatched first instars were used for experimental purposes.

Experimental design

One hundred eggs (50 of *C. septempunctata* and 50 of *C. transversalis*) were selected from the laboratory-reared stock and kept in Petri dishes (9.0 cm × 2.0 cm). After eclosion from eggs, neonates were taken from the Petri dishes and transferred to glass beakers containing *L. erysimi* infested host plant twigs of *Brassica campestris* Linnaeus.

Ten first instars (five of *C. septempunctata* and five of *C. transversalis*) were kept in each beaker. Instars were observed twice per day for moulting as well as mortality. As the instars moulted, the number of instars surviving to the next stage was recorded. Reduction in the number of instars suggested mortality; in cases where intact bodies of dead instars were obtained, they were considered as mortality due to abiotic factors or due to effect of prey quality; if no body or mutilated body was obtained then it was assumed to be a result of either cannibalism or IGP but it was not possible to differentiate between the two. The aphids were replenished daily and Petri dishes were changed to avoid any kind of infection. In this way survival, mortality and mortality factors for different life stages, namely eggs, first, second, third and fourth instars, pre-pupae and pupae were recorded. After eclosion, the adults of *C. septem-punctata* and *C. transversalis* were sexed on the basis of body size. Similar recordings were made in 10 replicates ($n = 10$).

Similar experiments were performed in the aphidophagous guild of two more aphids, namely *Myzus persicae,* and *Aphis nerii* from the host plants *Solanum nigrum* Linnaeus and *Calotropis procera* (Aiton), respectively.

Size and weight of both ladybirds were recorded to identify the predator and victim in both the ladybirds in cases of IGP. Body size was measured by placing the adults on a point on graph paper, holding them firmly but gently and the distances between the tip of the head and the abdomen were measured in 10 replicates ($n = 10$). Adults of both the ladybirds were then weighed (0.1 mg precision) using an electronic balance (SARTORIUS-H51; Shimadzu Corporation, Kyoto, Japan) ($n = 10$). Development periods of both *C. septempunctata* and *C. transversalis* were recorded in the aphidophagous guilds and data were subjected to one-way ANOVA (MINITAB, 2000).

The calculation of demographic parameters was made following Morris and Miller (1954):

x = The age interval, *i.e.* eggs, larvae, pupae and adults,
l_x = The number surviving at beginning stage,
d_x = The number dying within age interval x,
$100q_x$ = Apparent mortality, d_x as % of l_x,

$100r_x$ = Real mortality, d_x as a % of the original cohort size,

k = A dimensionless measure of the mortality within age interval of x, which was calculated using formula

k value = $\log_{10}l_x - \log_{10}l_x+1$,

where l_x initial number of individuals and l_x+1 = number of individuals surviving to next stage developing stages.

K (Kappa) = The total of k values,

S_x = Survival rate of a stage.

Generation survival values were also calculated (Harcourt, 1969).

$$\text{Generation survival} = \frac{\text{Number of female beetles}}{\text{Initial number of eggs}}\ .$$

Results

Body sizes of males and females of *C. septempunctata* were larger (5.22 ± 0.56 mm and 6.25 ± 0.68 mm, respectively) than of males and females of *C. transversalis* (5.00 ± 0.42 mm and 5.98 ± 0.52 mm, respectively). There was a significant difference in the body size of the male (F = 1.06; df = 1,18; $P < 0.2$) and female (F = 1.02; df = 1,18; $P < 0.2$) of both the ladybirds.

Male and female *C. septempunctata* were heavier (34.90 ± 2.44 mg and 39.05 ± 1.51 mg, respectively) than the male and female (31.93 ± 2.27 mg and 36.62 ± 2.55 mg, respectively) of *C. transversalis*. There was a significant difference in the weight of males (F = 7.96; df = 1,18; $P < 0.01$) and females (F = 6.70; df = 1,18; $P < 0.01$) of both the ladybirds.

The developmental period of *C. septempunctata* was significantly shorter (13.80 ± 0.34 d) than that of *C. transversalis* (16.95 ± 0.73 d) in the *L. erysimi* guild (F = 15.44; df = 1,8; $P < 0.005$) than that of *M. persicae* (F = 19.66; df = 1,8; $P < 0.005$) and *A. nerii* (F = 4.21; df= 1,8; $P < 0.01$; Fig. 1) guilds.

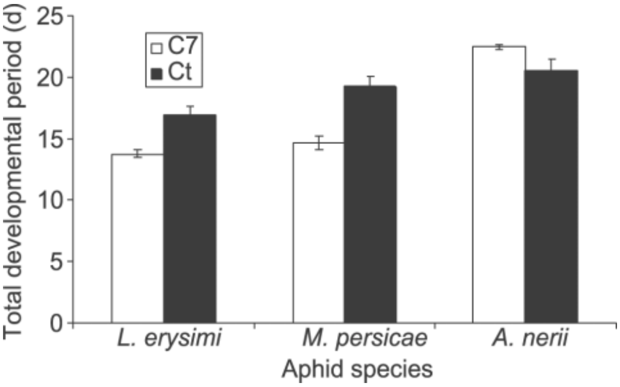

Fig. 1 Comparative graphs of developmental periods of the two ladybirds, *Coccinella septempunctata* (C7) and *C. transversalis* (Ct) in three aphid guilds.

Table 1 Mortality life table of *C. septempunctata* and *C. transvrsalis* on *L. erysimi.*

	X	l_x	d_x	$100q_x$	$100r_x$	S_x	Log Number	*k*- value
C. septempunctata	Eggs	50	0	0.00	0.00	1.00	1.699 0	0.000 0
	1st	50	2	4.00	4.00	0.96	1.699 0	0.017 7
	2nd	48	3	6.25	6.00	0.94	1.681 2	0.028 0
	3rd	45	3	6.67	6.00	0.93	1.653 2	0.030 0
	4th	42	2	4.76	4.00	0.95	1.623 2	0.021 2
	Prepupae	40	0	0.00	0.00	1.00	1.602 1	0.000 0
	Pupae	40	2	5.00	4.00	0.95	1.602 1	0.022 3
	Emergence	38					1.579 8	K = 0.119 2
	Male	18						
	Female	20						
C. transversalis	Eggs	50	0	0.00	0.00	1.00	1.699 0	0.000 0
	1st	50	12	24.00	24.00	0.76	1.699 0	0.119 2
	2nd	38	4	10.53	8.00	0.89	1.579 8	0.048 3
	3rd	34	3	8.82	6.00	0.91	1.531 5	0.040 1
	4th	31	1	3.23	2.00	0.97	1.491 4	0.014 2
	Prepupae	30	0	0.00	0.00	1.00	1.477 1	0.000 0
	Pupae	30	10	33.33	20.00	0.67	1.477 1	
	Emergence	20					1.301 0	K = 0.221 8
	Male	8						
	Female	12						

Apparent and real mortality parameters were highest for the first instar of all life stages in both the ladybirds in all aphidophagous guilds except *L. erysimi* where the mortality of second and third instars was higher (Tables 1−3). Pupal mortalities of *C. transversalis* were maximum (33.33% and 20.00%) in the aphidophagous guild of *L.*

Table 2 Mortality life-table of *C. septempunctata* and *C. transversalis* on *M. persicae*.

	X	l_x	d_x	$100q_x$	$100r_x$	S_x	Log Number	*k*-value
C. septempunctata	Eggs	50	0	0.00	0.00	1.00	1.699 0	0.000 0
	1st	50	4	8.00	8.00	0.92	1.699 0	0.036 2
	2nd	46	4	8.70	8.00	0.91	1.662 8	0.039 5
	3rd	42	2	4.76	4.00	0.95	1.623 2	0.021 2
	4th	40	0	0.00	0.00	1.00	1.602 1	0.000 0
	Prepupae	40	0	0.00	0.00	1.00	1.602 1	0.000 0
	Pupae	40	1	2.50	2.00	0.98	1.602 1	0.011 0
	Emergence	39						K = 0.107 9
	Male	14						
	Female	20						
C. transversalis	Eggs	50	0	0.00	0.00	1.00	1.699 0	0.000 0
	1st	50	9	18.00	18.00	0.82	1.699 0	0.086 2
	2nd	41	5	12.20	10.00	0.88	1.612 8	0.056 5
	3rd	36	6	16.67	12.00	0.83	1.556 3	0.079 2
	4th	30	4	13.33	8.00	0.87	1.477 1	0.062 1
	Prepupae	26	0	0.00	0.00	1.00	1.415 0	0.000 0
	Pupae	26	3	11.53	6.00	0.88	1.415 0	0.053 2
	Emergence	23					1.361 7	K = 0.337 2
	Male	10						
	Female	13						

Table 3 Mortality life-table of *C. septempunctata* and *C. transversalis* on *A. nerii*.

	X	l_x	d_x	$100q_x$	$100r_x$	S_x	Log Number	*k*-value
C. septempunctata	Eggs	50	0	0.00	0.00	1.00	1.699 0	0.000 0
	1st	50	25	50.00	50.00	0.50	1.699 0	0.301 0
	2nd	25	0	0.00	0.00	1.00	1.397 9	0.000 0
	3rd	25	2	8.00	4.00	0.92	1.397 9	0.036 2
	4th	23	0	0.00	0.00	1.00	1.361 7	0.000 0
	Prepupae	23	0	0.00	0.00	1.00	1.361 7	0.000 0
	Pupae	23	4	17.39	8.00	0.83	1.361 7	0.083 0
	Emergence	19					1.278 8	K = 0.420 2
	Male	10						
	Female	9						
C. transversalis	Eggs	50	0	0.00	0.00	1.00	1.699 0	0.000 0
	1st	50	40	80.00	80.00	0.20	1.699 0	0.699 0
	2nd	10	0	0.00	0.00	1.00	1.000 0	0.000 0
	3rd	10	0	0.00	0.00	1.00	1.000 0	0.000 0
	4th	10	0	0.00	0.00	1.00	1.000 0	0.000 0
	Prepupae	10	0	0.00	0.00	1.00	1.000 0	0.000 0
	Pupae	10	1	10.00	2.00	0.90	1.000 0	0.045 8
	Emergence	9					0.954 2	K = 0.744 7
	Male	4						
	Female	5						

erysimi than the other guilds (Table 2). The number dying within age interval (d_x), apparent mortality ($100q_x$) and real mortality of each stage was higher for *C. transversalis* than *C. septempunctata* in all three guilds.

Mortality prior to adult stage was minimum (1.60% and 3.20%, respectively) for *C. septempunctata* and *C. transversalis* in a guild of *L. erysimi* and maximum (6.20% and 8.20%, respectively) in a guild of *A. nerii*. In all three guilds, mortality prior to adult stage was lower for *C. septempunctata* than *C. transversalis*. Generation survival of *C. septempunctata* and *C. transversalis* was highest (0.46 and 0.40) in the guild of *L. erysimi* and lowest (0.18 and 0.10) in the guild of *A. nerii* (Table 4).

The kappa values for *C. septempunctata* and *C. transversalis* were 0.119 2 and 0.221 8, respectively in the *L. erysimi* guild, 0.107 9 and 0.337 2, respectively in the *M. persicae* guild and 0.420 2 and 0.744 7, respectively in the guild of *A. nerii*. The sex ratio of emerging adults was female-biased in guilds of *L. erysimi* and *M. persicae* for both the ladybirds while it was male-biased in the guild of *A. nerii* (Table 4).

Discussion

The results from the life table studies of two congeneric ladybirds in the aphidophagous guilds of three aphid species revealed that the prey quality and size of predator affected the stable coexistence of developing stages of both ladybirds. The difference in mortality and survival rate of developing stages amongst guilds might be due to difference in prey suitability, which depends on the physiological status of the host plant, energy requirements and nutritional budgets (Soares *et al*., 2004).

Among the developing stages, the first instar of both ladybirds was most sensitive to food quality and vulnerable to mortality factors. Maximum mortality of first instars of both ladybirds was found in the guild of *A. nerii* than other guilds. Non-occurrence of bodies and residues of first instars of *C. transversalis* is the reason for expecting cannibalism and/or IGP to be the causes of mortality. Despite high levels of protein (Atwal & Sethi, 1963) and higher consumption of *L. erysimi* (Omkar & Srivastava, 2001) larval mortality was observed in this guild, albeit relatively lower in comparison to other guilds. The results indicate that there is an innate tendency of instars to attack the soft-bodied siblings even in the presence of adequate food supply, especially during the early instars, which is also supported by the results of Shands *et al*. (1970). The comparatively lower mortality of the older instars suggests that risk of being cannibalized by older instars exists on attacking the conspecifics as well as heterospecifics, as larvae presumably assess their hunger (Dixon, 2000). Prior to investigation, it was assumed that the guild of *A. nerii*, probably would not fulfill the nutritional requirement, and therefore development of instars will be hampered. In support of our assumption the first instars were unable to cope with the probable increased toxicity levels of *A. nerii*. A high amount of cardiac glycosides, cardenolides, particularly oleandrin and nerii, were known to be responsible for the toxicity of *A. nerii* obtained from the host plant, *Nerium oleander* (Rothschild, 1961). Increased hunger of first instars due to the non-availability of essential prey or the scarcity of accepted prey probably resulted in cannibalism and/or IGP.

Although in this study mortality in ladybirds could not be differentiated accurately into cannibalism and IGP, mutilation of instars is more likely to support their incidence. Comparatively lower mortality in each guild, larger size and greater weight of *C. septempunctata* help us in assuming that probably in these guilds, *C. septempunctata* acts as intraguild predator and *C. transversalis* as the intraguild prey. These findings are confirmed by earlier studies which suggest that in most cases of cannibalism or IGP, the differences in the size determine the consequence of the interaction in which smaller individuals are killed by the larger ones (Agarwala & Dixon, 1992; Snyder & Hurd,

Table 4 Life table parameters of *C. septempunctata* and *C. transversalis* in three aphidophagous guilds.

		C. septempunctata	*C. transversalis*
L. erysimi	% Mortality prior to adult stage	1.60	3.20
	Generation survival	0.46	0.42
	Sex ratio	0.51	0.57
M. persicae	% Mortality prior to adult stage	2.20	5.40
	Generation survival	0.40	0.26
	Sex ratio	0.55	0.62
A. nerii	% Mortality prior to adult stage	6.20	8.20
	Generation survival	0.18	0.10
	Sex ratio	0.47	0.56

1995; Lucas *et al*., 1997). Faster growth rate of larvae of *C. septempunctata* may also help them in acting as intraguild predators. Earlier studies also support these findings (Kawauchi, 1985; Obrycki *et al*., 1997; Srivastava & Omkar, 2004).

In a guild of *Harmonia axyridis* and *C. septempunctata* there was a tendency of the former to act as intraguild predator while the latter acted as intraguild prey; cannibalism was also observed in both species (Yasuda *et al*., 2001). However, in a guild of *C. septempunctata* and *Cycloneda maculata*, the former, which is larger in size, had a higher rate of survival (Obrycki *et al*., 1997). In the present study, only larvae of *C. septempunctata* were noticed attacking the larvae of *C. transversalis* during random observations; the reverse was not observed, indicating asymmetrical IGP along with innate cannibalistic tendencies to be the probable reasons for a major part of the recorded mortality. Asymmetrical IGP may be related to the differences in food specificity and vulnerability between the two species (Yasuda & Katsuhiro, 1997). Cannibalism and IGP are likely to be adapted to ensure their survival in the absence, scarcity or toxicity of prey.

On high quality prey *L. erysimi*, rate of cannibalism and intra guild predation were less for *C. transversalis*. These incidences increased on prey of intermediate quality (i.e. *M. persicae*) and were highest on low quality food (i.e. *A. nerii)*. The study suggests that developmental stage, vulnerability, size and hunger of conspecific/ heterospecific determine cannibalism/IGP. These are probably initiated by the hunger but their rates are governed by the prey scarcity, prey availability and prey quality (Michaud, 2003; Pervez *et al*., unpublished data). The feeding specificity of the predator is also an important factor influencing the outcome of intraguild interactions as specialist predators were more likely to become intraguild prey (Lucas *et al*., 1998). The findings are in close agreement with Snyder *et al*. (2000) as larvae of *H. axyridis* developed faster when fed on prey of intermediate quality and did not complete their development on low quality prey unless their diet included conspecifics. Some reports reveal that cannibalism is driven more by reduced food availability than by reduced food quality (Michaud, 2003; Pervez *et al*., unpublished data).

Sex ratio, that is the proportion of females in the population, of *C. septempunctata* and *C. transversalis* was highest on the prey *M. persicae* and *L. erysimi*, respectively. It revealed the probable role of prey species in determining sex ratio. Earlier it was found that when *C. septempunctata* were fed on alfalfa aphids, a higher female-biased ratio occurred (Azam & Ali, 1970). Progeny of *Propylea 14-punctata* was also found to show different sex ratios on varying food types (Rogers *et al*., 1972).

The findings revealed that the rate of cannibalism and IGP in abundant supply of high prey quality is less and increased with the decline in prey quality. Early instars tend to be victims of cannibalism and IGP even under adequate food supply. Larger size and higher weight of *C. septempunctata* suggests that it probably acted as an intraguild predator, and *C. transversalis* due to its smaller size and less weight, became the intraguild prey in the guilds of *L. erysimi* and *M. persicae*. *Coccinella transversalis* developed faster than *C. septempunctata* on *A. nerii* (lower quality prey) thus indicating that this aphid is probably more suitable to *C. transversalis*. High survival rate of all stages of *C. septempunctata* than *C. transversalis* in all the three guilds suggests the dominance of *C. septempunctata* in assemblages of congeneric ladybirds and this supports their probable role in displacement of other ladybird species, wth the exception of *Harmonia axyridis* Pallas, the world over.

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