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REVIEW ARTICLE

Prey-Predator Relationships in Ladybird Beetles and Biological Control of Insect Pests

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ABSTRACT

Members of family Coccinellidae, commonly known as ladybirds, are the predaceous insects that are polyphagous in nature. Their prey range is categorised as essential, alternative or rejected. Ladybirds fed essential prey survive better as larvae and are more fecund as adults, whereas those fed on alternate prey are only able to survive without growth and reproduction. Rejected prey species are unpalatable due to their intensive/aposematic colourations and/or presence of certain allelochemicals. Consequently, they are rejected even after encounters. Certain prey species are even harmful to ladybirds, causing their mortality, and are termed as toxic prey species. Ladybirds accept some prey species that are not adequate and worsen their life-history parameters, although they are not toxic and are considered 'problematic prey'. While the prey of ladybirds is classified as essential, alternative, rejected and toxic, ladybirds prefer essential prey to perform their best in terms of egg maturation, oviposition and development. However, numerous other factors may affect the prey preferences of ladybirds, and include: (i) prey species, (ii) prey abundance, (iii) morphology, mobility and defence of prey, (iv) learning ability, memory, morphological character and previous feeding experience of predator, (v) environmental factors (temperature and photoperiod), and (vi) genetic factors. While ladybirds locate their prey by extensive search, butswitch to intensive search once the feeding of prey initiates. If no further prey are captured, these predators gradually change their prey search mode from intensive to extensive again. During both extensive and intensive searches, ladybirds sense both environmental and inner cues that orientate them toward their prey. However, both abiotic (temperature, humidity, light intensity) and biotic factors (prey, other predators and their interactions) affect the searching behaviour of ladybirds by modifying their rate of movement. Thus, the biocontrol programmes can only be benefitted if all such factors that affect prey-predator relationships in Coccinellidae are fully explored prior to the selection of ladybird species for their mass multiplication in laboratories.

KEY WORDS: Biocontrol, Environment, Ladybirds, Prey-predator relationship

INTRODUCTION

Food is the crucial fundamental factor that determines an insect's growth, development and reproduction. Both the quality and quantity of prey significantly influence the life history traits of insects at the individual and species levels (Blackenhorn, 2000). Coccinellids (Coleoptera: Coccinellidae), commonly known as ladybeetles, ladybird beetles or ladybirds, are an important group of insect predators with considerable potential tobe used as biocontrol agents of aphids and other insect pests (Hodek & Honek, 1996; Michaud, 2012; Rosagro *et al*., 2019). They feed on a wide range of prey, tend to be very voracious and exhibit rapid functional and numerical responses (Hodek & Honek, 1996; Bayoumy, 2011; Bayoumy & Michaud, 2012; Pervez *et al*., 2018). Their food range includes sternorrhynchan Hemiptera, Thysanoptera, phytophagousmites, young instars of holometabolous insects and even fungi (Evans, 2009; Hodek *et al*., 2012), which has resulted in their categorisation as either aphidophagous, coccidophagous, acarophagous or

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*Corresponding author email: omkar.lkouniv@gmail.com mycophagous. Although ladybirds are best at exploiting aphids (Pettersson *et al*., 2005; Evans, 2008), but due to the short life span and patchy distribution of aphids, their availability is quite uncertainin agricultural fields (Hodek *et al*., 2012).

Under such scarce prey conditions, many predaceous ladybirds use non-prey foods as integral components of their diet to increase their survival. The non-prey range includes nectar, honeydew, pollen, fungal spores and vegetation (Omkar, 2006; Lundgren, 2009; Sutherland & Parella, 2009). Gut dissections of field-collected ladybirds have revealed their frequent consumption of inorganic materials (Triltsch, 1999), but the role of these inorganic materials in the nutritional ecology of ladybirds is entirely unknown. Frequent aggregation of *Harmonia axyridis* (Pallas) on grapes, apples, peaches, plums, pears, pumpkins and raspberries, resulting in their damage are also in records (Koch *et al.*, 2005; Pervez & Omkar, 2006; Koch & Galvan, 2008). Feeding on fungal spores by ladybirds is assumed to be associated with early evolution ofaphidophagy, *i.e.* ladybirds consuming the honeydew producing sternorrhynchans first consumed the sooty moulds (Lundgren, 2009) (Fig. 1).

Not only do ladybirds consume the above mentioned variable non-prey species, they are also engaged in cannibalism and intraguild predation (IGP) at times (Toosi *et al*., 2019). When the abundant prey is less or its nutritional quality decreases, both cannibalism and IGP are the alternative ways to sustain and promote development and survival (Polis, 1981; Snyder *et al.*, 2000; Kumar *et al*., 2014b). Cannibalism enables ladybird larvae to optimally utilize the resources in a patch, and IGP results in the dominant species monopolising the resources and a decrease in the abundance of competitors (Dixon, 2000; Hodek *et al*., 2012; Ovchinnikov *et al*., 2019). Thus, both these mechanisms determine the efficiency with which the resources at a specific feeding site are utilised. Under such circumstances, aphid prey is less attacked in agricultural fields, and the ladybird species show predatory interactions (Phoofolo & Obrycki, 1998). Cannibalism has also been reported even in the presence of *ad libitum* aphids (Agarwala & Dixon, 1992). Thus, feeding on non-prey species can provide initial advantages to the ladybirds in fulfilling their nutritional requirements, to complete their development, to get them their first meal or to eliminate their potential competitors.The non-prey range of ladybirds are widespread and easy to be encountered, but are substantially less suitable for them.

In this attempts have been made to establish prey-predator relationships in family Coccinellidae. On completion of, it is expected that readers will be aware of the prey classification, factors affecting the prey preference, and the foraging behaviour of the members of family Coccinellidae. We anticipate that the views

Fig. 1. Members of family Coccinellidae feeding on aphid prey

presented in the would be utilized to mass multiply ladybirds in research laboratories/insectaries for their use in augmentative biocontrol programs against the pests of agricultural importance.

Prey classification of Coccinellidae

The broad prey range of aphidophagous ladybirds is categorised as: (i) essential, (ii) alternative (accepted but sub-optimum), or (iii) rejected (Hodek, 1996). This classification is based on the growth, development, survival and reproduction of the ladybirds when fed on different aphid species. Ladybirds feeding on essential prey survive better as larvae and are more fecund as adults, whereas those feed on alternate prey are only able to survive without growth and reproduction (Hodek, 1962; Mills, 1981; Hodek, 1996). Essential prey are further classified into optimal, adequate and marginal (Michaud, 2005), based on the differences in their nutritive values and the ways by which these nutrients are assimilated and utilised post prey consumption (Phoofolo *et al*., 2007; Castro-Guedes *et al*., 2016; Gupta & Kumar, 2017) (Fig. 2).

Rejected prey species are unpalatable due to their intensive/ aposematic colourations and presence of certain allelochemicals. Consequently, they are rejected even after encounters (Hodek, 1996). Malcolm (1992) introduced the terms included, peripheral and excluded for essential, alternative and rejected prey. The prey selected by ovipositing females for their larvae are termed as ‘nursery prey’ (Dixon, 2000) and are the species of prey on which the larvae are likely to develop the best in terms of survival and growth (Wilder *et al.*, 2010). Studies have also suggested a “mixed diet” composed of “essential” and “alternative” prey for better survival of ladybird predators (Kianpour *et al.*, 2011; Schuldiner-Harpaz & Coll, 2017).

Rana *et al*. (2002) reported the cost of prey specialisation of ladybird, *Adalia bipunctata* (L.). They reared thespecies for six generations on its more suitable aphid prey, *Acyrthosiphon pisum* (Harris) and a less suitable one, *Aphis fabae* Scopoli. They found that with furtherance of generations, the mortality of ladybirds on *A. fabae* reduced from 53.8% in the first generation to 0% in the sixth one. On shifting the offspring of the sixth generation reared on *A. fabae* to suitable prey *A. pisum*, high mortality was recorded indicating specialisation and conditioned preference of the ladybird for its previously less suitable prey. The study thus indicated that feeding preferences and prey suitability of ladybirds are a result of the duration of contact and the relationships between the predator and the prey. Soares *et al*. (2004) demonstrated the process of dietary self-selection in the ladybird, *H. axyridis.* On being provided with mixed populations of aphid, *A. fabae* and *Myzus persicae* (Sulzer) at different densities, voracity of *H. axyridis* was found to be increased with an increase in proportion of *M. persicae* in the provided prey population. Although, males showed a constant preference for *M. persicae*, but this was not the case with females.

Certain prey species are also harmful to ladybirds, causing their mortality, and are termed as toxic prey species (Nedved & Salvucci, 2008). Studies have shown that the aphid species, *Aphis sambuci* L., feeds on elder, *Sambucus nigra* Elder, which contains toxic compounds and the aphids sequester these compounds from the host plant. One of the toxins is cyanoglycoside sambunigrin, producing hydrocyanate after enzymatic splitting (see Nedved & Salvucci, 2008). Another potentially toxic compound is alkaloid sambucine (Auster & Schafer, 1956). Thus, the aphid species that have been found to be toxic for some ladybirds, either cause gradual poisoning (e.g. *A. sambuci*), or an acute toxic effect (e.g. *Aphis nerii* Boyer de Fonscolombe feeding on *Nerium oleander* L.) (Iperti, 1966) in ladybirds. In addition, ladybirds even feed on certain prey species that are not adequate and worsen their life-history parameters, although the prey species

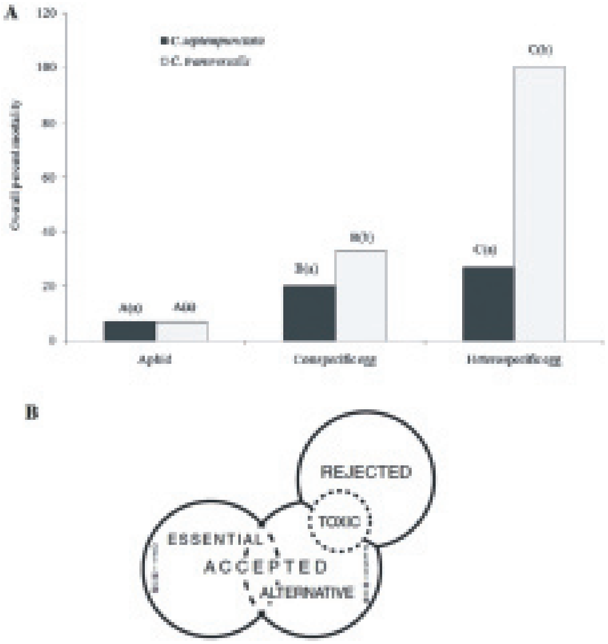


Fig. 2. (A)Percent overall mortality of ladybird larvae when fed on aphid (essential prey) and conspecific/ heterospecific eggs (alternative food); and (B) Types of physiological suitability of ladybird beetles (see Kumar *et al*., 2014b; Hodek *et al*., 2012).

are not toxic but are considered as 'problematic prey' (Hodek *et al.*, 2012). The adults and larvae of *A. bipunctata* were occasionally found feeding on tetranychid mites but could not complete their development on the prey (Robinson, 1951). By changing the diet between larvae and adults of the highly polyphagous ladybird, *Coleomegilla maculata lengi* De Geer, Michaud & Jyoti (2008) revealed 'dietary complementation across the life stages'. Likewise, similar findings were observed by Hamasaki & Matsui (2006) on ladybird, *Propylea japonica* (Thunberg), when fed on *Ephestia kuehniella* Zeller eggs combined with pea aphids.

Factors affecting prey preference in Coccinellidae

1. Prey species

Prey suitability in ladybirds is assessed on the basis of predation attributes, growth, development and reproduction (Kalushkov & Hodek, 2001; Stamp & Meyerhoefer, 2004; Berkvens *et al.*, 2010; Sarwar & Saqib, 2010; Kumar *et al.*, 2013; Papachristos *et al.*, 2015). The comprehensive approach to evaluate prey suitability of ladybirds in terms of preference (prey biomass consumed and oviposition site selection), performance (development, survival, reproduction, mortality and fertility life tables, and individual fitness levels of predator), and preference–performance correlations was adopted by Omkar & Mishra (2005). High quality and most suitable prey as a food is beneficial to ladybirds in providing them with better growth and development, and lower mortality (Stamp & Meyerhoefer, 2004; Omkar & Mishra, 2005; Omkar *et al.*, 2009a, 2011; Dixon *et al.*, 2011; Bista & Omkar, 2013; Kumar *et al.*, 2013; Patel *et al.*, 2017; Canovai *et al.*, 2019). Investigations on food assimilation and energy allocation have revealed the high rates of conversion efficiencies and growth rates in ladybirds when fed on high quality prey (Mishra *et al.*, 2011, 2012a; Kumar *et al.*, 2014b). Studies have further revealed that the most suitable prey species contain higher levels of proteins and absence of unsuitable chemicals (Atwal & Sethi, 1963; Kumar *et al.*, 2013). In contrast, the least suitable species sequester chemicals from their host plants, which contain certain alkaloids that are toxic for many ladybirds (Hodek, 1956; Okamoto, 1966), and the ladybirds avoid feeding on such prey species (Kumar *et al.*, 2013).

Ladybirds that are efficient in converting prey biomass to their own biomass are also efficient reproducers, and are believed to convert prey biomass maximally to their progeny (Omkar *et al.*, 2005a). Higher fecundity, egg fertility, clutch number and clutch size of *C. septempunctata* and *C. transversalis* on *A. pisum* and *A. craccivora*, respectively, substantiate towards the presence of better and essential nutrients in these aphid species for the respective ladybirds that result in their higher palatability. However, it took several generations for *C. septempunctata* to get adapted to deal with *A. pisum* toxins, and for *C. transversalis* to become well used to *A. craccivora*, and acquire the ability to detoxify the toxins of their prey (Bista & Omkar, 2013).

Prey quality and its suitability to individual ladybirds, *viz. A. bipunctata* (Ferrer *et al.*, 2008), *Anegleis cardoni* (Weise) (Omkar *et al.*, 2009a, 2011), *Brumoides suturalis* (Fabricius) (Bista *et al.*, 2012; Lima *et al.*, 2017), *Chilocorusbi pustulatus* (L.) (Uygun & Elekcioglu, 1998), *C. septempunctata* (Omkar & Srivastava, 2001, 2003a, b; Srivastava & Omkar, 2004; Kianpour *et al.*, 2011; Bista & Omkar, 2013; Kumar *et al.*, 2013, 2015), *C. transversalis* (Omkar & James, 2004a; Gupta *et al.*, 2006; Bista & Omkar, 2013; Kumar *et al.*, 2013, 2015), *H. axyridis* (Osawa, 1989; Castro-Guedes *et al.*, 2016); *Menochilus sexmaculatus* (F.) (Omkar & Bind, 2004; Patel *et al.*, 2017), *Hyperaspis notata* Mulsant (Dreyer *et al.,* 1997), *Micraspis discolor* (Fab.) (Omkar & Pervez, 2001; Omkar, 2006), *P. dissecta* (Mulsant) (Pervez & Omkar, 2004a; Omkar & Mishra, 2005), *P. japonica* (Zhang *et al.*, 2007), *Propylea quatuor decimpunctata* (L.) (Keshavarz *et al.*, 2015), *Rodoliaiceryae* Janson (Kairo & Murphy, 1995), *Sphaerobothria hoffmanni* Karsch (Kawauchi, 1985), or within conspecific/heterospecific groups (Omkar *et al.*, 2005b; Kumar *et al.*, 2015) have been well documented and their prey suitability has been studied in terms of developmental attributes, life table parameters and reproductive performances. Numerous studies in literature have also assessed the prey quality in terms of mortality life table parameters (Iverson & Hardling, 2007; Nielsen *et al.*, 2008; Haye *et al.*, 2010; Borges *et al.*, 2011; Kianpour *et al.*, 2011; Ugine & Todd, 2012). The results of all such studies thus indicate that growth, development, reproductive performance, and longevity are highest on the most suitable prey and lowest on the least suitable prey (Table 1).

Predatory performance of ladybirds has also been studied in terms of prey consumption rates or voracities (Omkar & Srivastava, 2001, 2003a, b; Finlayson *et al.*, 2010; Kumar *et al.*, 2013; Patel *et al.*, 2017), consumption indices, conversion efficiencies and/or growth rates (Lundgren & Weber, 2010; Kumar *et al.*, 2013; Patel *et al.*, 2017; Jalali *et al.*, 2019). These studies have shown that all prey species are not equally suitable for ladybirds (Omkar *et al.*, 2011; Zhang *et al.*, 2012; Bista & Omkar, 2013), and the ladybirds perform best on the highly palatable prey. Moreover, highly palatable prey species diminishes the population pressure on the larvae, resulting in their fast

Table 1: Developmental parameters of a ladybird, *A. cardoni* when fed on different aphid species (see Omkar *et al*., 2011)

	Developmental parameters							
Aphid species	Immature survival(%)	Pupation (%)	Female wt (mg)	Male wt (mg)	Development rate	Growth index	Generation survival	Sex ratio
U compositae	90.00±4.47b	90.00±4.47a	7.39±0.24c	6.96±0.25c	0.039±0.00d	6.05±0.30b	0.44±0.06a	0.47±0.05
R. maidis	88.00±4.42b	90.00±4.47a	7.11±0.20bc	6.64±0.23c	0.038±0.00cd	5.92±0.29b	0.50±0.04a	0.57±0.05
H. coriandri	88.00±6.11b	90.00±4.47a	6.90±0.15bc	6.21±0.17bc	0.037±0.00cd	5.83±0.29b	0.48±0.07a	0.56±0.07
M. persicae	90.00±4.47b	92.00±4.42a	6.86±0.24bc	5.81±0.29b	0.037±0.00c	5.84±0.28b	0.46±0.06a	0.50±0.06
A. pisum	86.00±4.27b	88.00±4.42a	6.40±0.22b	5.86±0.24b	0.036±0.00c	5.51±0.28b	0.42±0.04a	0.48±0.03
R. padi	86.00±5.21b	88.00±4.42a	6.22±0.27ab	5.50±0.25ab	0.035±0.00bc	5.24±0.26b	0.42±0.04a	0.49±0.03
B. brassicae	82.00±5.54ab	86.00±5.21a	5.93±0.21ab	5.22±0.15ab	0.034±0.00b	4.89±0.30ab	0.42±0.04a	0.52±0.04
H. setariae	74.00±5.21ab	80.00±4.22a	5.81±0.12ab	5.14±0.16ab	0.033±0.00ab	4.40±0.23ab	0.36±0.03a	0.49±0.03
C. silvestri	64.00±5.81a	74.00±6.00a	5.56±0.17a	4.90±0.14a	0.032±0.00a	4.00±0.32a	0.32±0.05a	0.50±0.09
F-values	2.87*	1.47 NS	9.25**	10.55*	25.63**	6.43**	1.36 NS	0.41NS

Values are means (±SE). Different letters per column indicate values to be statistically different.
* and ** indicate *F*-values to be significant at $P < 0.01$ and $P < 0.001$, respectively; Tukey's test range = 4.51; df = 8, 89.
NS indicates *F*-values to be non significant at $P > 0.05$

pre-imaginal development (Omkar & James, 2004a; Ferrer *et al.*, 2008; Maurice & Kumar, 2012; Bista & Omkar, 2013). Further, within aphidophagous guilds formed by the larvae and adults of the ladybird species exploiting the same prey resource (Yasuda & Shinya, 1997; Dixon, 2000), abundance of highly palatable and most suitable prey species reduces the incidences of cannibalism and IGP (Agarwala & Dixon, 1992; Snyder *et al*., 2000; Cottrell, 2005; Kumar *et al*., 2014b)(Fig. 3; Table 2).

While evaluating the performance of ladybird, *A. cardoni* on three aphid prey, *viz. Aphis gossypii* Glover, *A. craccivora* and *Lipaphis erysimi* Kaltenbach, Omkar *et al*. (2009a) found the reproductive rate and intrinsic rate of increase to be highest on *A. gossypii* and lowest on *L. erysimi.* Life table data generated by Omkar *et al*. (2011) on ten aphid species using *A. cardoni* as the ladybird predator revealed that the overall mortality of *A. cardoni* larvae prior to adult stage was lowest when fed on *Uroleucon compositae* (Theobald) and highest on *Ceratovacuna silvestri* (Takahashi). Bista *et al.* (2012) evaluated the development and survival rates of ladybird, *B. suturalis*, on two aphid species, *A. pisum* and *A. gossypii*, and found that the immature stages developed faster on *A. pisum*, but the survival of early instars was higher on *A. gossypii*. However, when evaluated the fertility life table of *Hippodamia variegata* (Goeze) on three aphid prey (*i.e. A. gossypii*, *A. fabae* and *M. rosae*), Golizadeh & Jafari-Behi (2012) reported highest and lowest net reproduction rates (R_0) of the beetle on *A. fabae* and *Macrosiphum rosae* (L.), respectively. Studies on life-history traits of *C. transversalis* and *C. septempunctata* indicated the pea aphid, *A. pisum*, to be the most suitable prey for *C. septempunctata* and the bean aphid, *A. craccivora*, for *C. transversalis* (Kalushkov & Hodek, 2004; Bista & Omkar, 2013).

Keshavarz *et al*. (2015) assessed the feeding preferences of individuals from two populations of *P. quatuordecimpunctata* on *A. fabae* and *A. gossypii*. Their results revealed that *P. quatuordecimpunctata* from the two different populations preferred *A. gossypii* over *A. fabae*. Moreover, Kumar *et al*. (2013, 2015) reported higher predation attributes of *C. transversalis* larvae on *A. craccivora* and *C. septempunctata* larvae on *L. erysimi*; but when the larvae of both the predators were kept in heterospecific combinations, they exhibited additive effects on *L. erysimi* but antagonistic effects on *A. craccivora*. In contrast, Patel *et al*. (2017) found higher predation attributes of *M. sexmaculatus* larvae on *A. craccivora* than on *L. erysimi* under prey fluctuating conditions. Hosseini *et al*. (2019) reported that by manipulating the quality of host plant (fertilised with different nitrogen levels), life history parameters in *Hippodamia variegata* were altered on its prey, *Aphis gossypii*. Lifetime aphid consumption and intrinsic rate of increase in the ladybird were lowered when the host plants were treated with fertilizers containing high nitrogen content than those treated with medium or low nitrogen content. Previous literature, therefore, suggest that prey species may differ in terms of their physical structure, size, chemical defence, behaviour, ability to escape capture and ability to derive nutrients from the host plants. Each of these features can affect the selection of particular prey by ladybirds in natural and artificial agroecosystems.

2. Prey abundance

Prey-predator relationships involving aphidsand ladybird predators are well documented. Since aphid availability in agroecosystems often fluctuates in space and time, its deprivation severely affects the life attributes of ladybirds (Omkar & Pervez, 2003; Phoofolo *et al.,* 2008; Santos-Cividanes *et al.,* 2011; Chaudhary *et al*., 2015; Patel *et al*., 2017). As a result, predatory responses of ladybird species differ under variable quantities of prey (Table 3). Such variations in predatory behaviour of ladybirds govern complex interactions (e.g. intra- and inter-specific competitions) between them when preying on a common prey resource. Therefore, investigation on the intensity and nature of such interactions between ladybird predators in relation to prey scarcity or abundance is of great relevance as they may affect the structures of predatory guilds.

2.1. Functional and numerical responses : Majority of the studies on prey quantity have evaluated the functional responses of ladybirds under variable prey density to understand the interactions between predaceous ladybirds and their prey species (Omkar & Kumar, 2013; Kumar *et al*., 2014a; Chaudhary *et al*., 2015; Patel *et al*., 2017; Jalali & Ziaaddini, 2017; Wu *et al*., 2018; Crookes *et al*., 2019). Solomon (1949, 1964) proposed the concept of a predator's functional response as the rate of prey consumption (*i.e.* number of prey consumed per unit time) as a function of prey density. Later on, Holling (1959a,b, 1965) proposed three basic types of functional responses, which reflect that the number of prey consumed by a predator as prey density increases may increase linearly (type I), in a decelerating fashion (type II) or in a sigmoidal fashion (type III). However, studies report five types of predatory response curves, *viz*. Type I, which is linear, Type II, which is curvilinear, Type III, which is sigmoidal (Holling, 1959), Type IV, which is dome shaped (Luck, 1985; Bressendorff & Toft, 2011) and Type V, which is negative exponential (Sabelis, 1992). But majority of them reveal Holling's Type II functional response in ladybirds (e.g., Omkar & Pervez, 2011; Gupta *et al.*, 2012; Omkar & Kumar, 2013; Chaudhary *et al*., 2015; Latifian, 2017; Qin *et al*., 2017; Rahimi *et al*., 2017), characterised by a curvilinear shape, where a predator is assumed to feed on

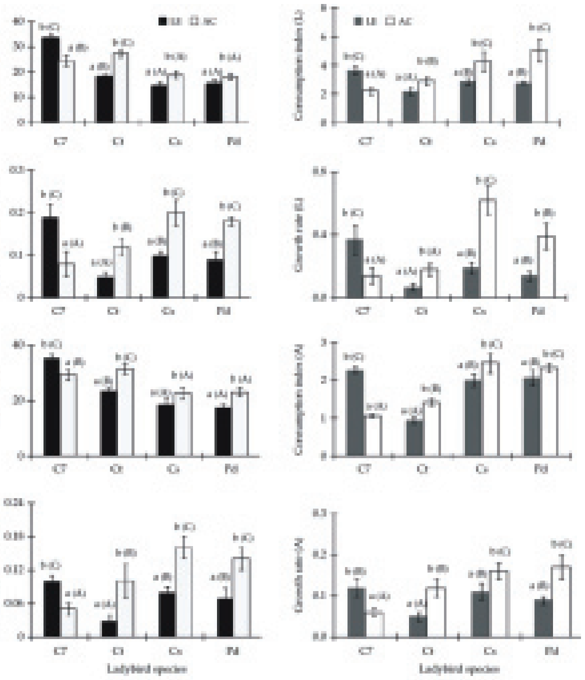


Fig.3. Comparative predation attributes of *C. septempunctata* (C7), *C. transversalis* (Ct), *M. sexmaculatus* (Cs) and *P. dissecta* (Pd) on aphid species, *A. craccivora* (AC) and *L. erysimi* (LE)(see Kumar *et al*., 2013)

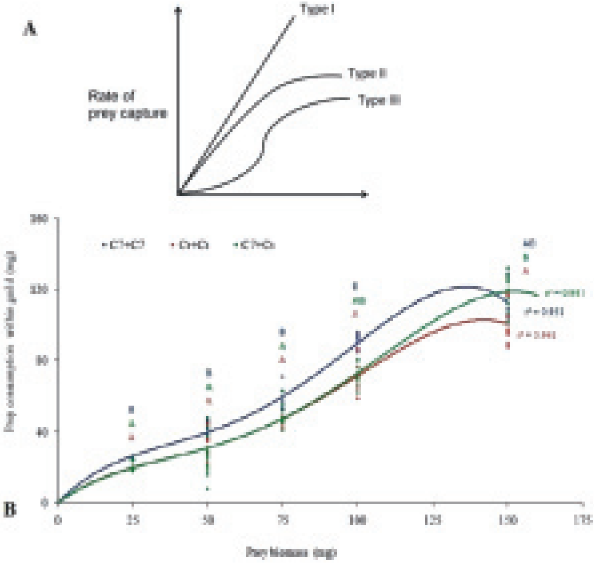


Fig. 4. (A) Functional response curves common in members of family Coccinellidae; (B) Modified type-II functional response curves of ladybirds kept within conspecific/ heterospecific guilds (see Kumar *et al*., 2014a)

Table 2: Predatory interaction on different prey species within aphidophagous guilds (see Kumar *et al.,* 2015)

				Multiplicative Risk model			
Aphid prey species	Predatory combinations	Combined prey consumption(mg)	Sum of individual prey consumptions(mg)	Observed prey consumption(%)	Expected Prey consumption(%)	F-value (P-value)	Predatory interaction
A. pisum	C7 + C7	62.53±1.72	89.00±4.00	62.53±1.72^{Aa}	97.44±2.07	168.14(<0.0001)	Antagonism
	C7 + Ct	62.04±1.66	70.40±4.22	62.04±1.66^{Aa}	89.63±2.70	75.64(<0.0001)	Antagonism
	C7 + Ct	68.40±3.80	79.90±2.00	68.40±3.80^{Ba}	97.70±0.40	59.74(<0.0001)	Antagonism
A.craccivora	C7 + C7	62.04±1.66	90.76±1.04	62.04±1.66^{Aa}	99.05±0.17	492.93(<0.0001)	Antagonism
	Ct + Ct	66.32±1.88	53.63±5.70	66.32±1.88^{Ba}	75.57±5.81	2.30(0.147)	Additive
	C7 + Ct	67.00±2.42	72.20±2.84	67.00±2.42^{Ba}	95.78±0.80	127.62(<0.0001)	Antagonism
L. erysimi	C7 + C7	66.32±1.88	60.36±3.89	66.32±1.88^{Ba}	82.93±3.34	18.76(<0.0001)	Antagonism
	Ct + Ct	61.36±1.29	50.97±2.29	61.36±1.29^{Aa}	75.49±2.28	29.08(<0.0001)	Antagonism
	C7 + Ct	68.00±3.69	55.67±2.21	68.00±3.69^{Ba}	80.61±2.01	8.99(0.008)	Antagonism

i. C7 and Ct represent *Coccinella septempunctata* and *Coccinella transversalis,* respectively.

ii. Large letters compare observed prey consumption among predatory combinations per aphid species and small letters compare observed prey consumption between aphid species per predatory combination, based on Tukey's post hoc comparison of means.

prey without any initial delay in learning ways to avoid difficulties (Sarmento *et al.*, 2007).

When kept individually, the functional response is not stage specific and both larvae and adults show similar curves (Omkar & Srivastava, 2001, 2002; Omkar & Kumar, 2013); characterised by an increased predation with increase in prey density, reaching an asymptote at higher prey densities and thereafter remains unaffected due to satiation (Mills, 1982; Jeschke *et al.*, 2002, Jalali *et al.*, 2010). In addition, some studies have reported a modified Type II functional response, i.e consisting of a decelerating (type II) functional response when provided with low to optimal supply ofprey, followed by an accelerating (type III) functional response when provided with an optimal to abundant supply of prey (Kumar *et al.*, 2014a; Chaudhary *et al.*, 2015; Patel *et al.*, 2017). A few studies have also found Type III response (*i.e.* sigmoidal curve) in ladybirds (e.g., Sarmento *et al.*,2007; Abdollahi *et al.*, 2010; Latifian, 2017), where a predator is assumed to learn to evade the difficulties associated with prey capture (Schenk & Bacher, 2002) (Fig. 4).

In recent years, functional responses have been viewed broadly as the rate of prey consumption of an individual predator (Hodek *et al.*, 2012). The functional response can accordingly be modeled, as it varies not only with the prey density, but also with other interacting factors (which may influence predator foraging), such as predator density (Mills & Lacan, 2004; Schenk *et al.*, 2005), densities of alternate prey (e.g. Tschanz *et al.*, 2007), densities of the predator's natural enemies (e.g. Krivan & Sirot, 2004), foraging substrate and abiotic conditions (Jalali *et al.*, 2010; Khan & Khan, 2010). Moreover, the functional response alone does not provide sufficient information about the population level effects of natural enemies. Thus, to predict the influence of prey density on oviposition, the numerical responses of ladybird species need to be studied. In this regards, several studies have evaluated the functional and/or numerical responses of ladybird species individually (Sarmento *et al.*, 2007; Abdollahi *et al.*, 2010; Bayoumy, 2011; Bayoumy & Michaud, 2012; Omkar & Kumar, 2013; Patel *et al.*, 2017; Jalali & Ziaaddini, 2017; Rahimi *et al.*, 2017) and within guilds (Snyder & Ives, 2003; Costamagna *et al.*, 2007; Snyder, 2009; Omkar & Pervez, 2011; Kumar *et al.*, 2014a; Chaudhary *et al.*, 2015).

Solomon (1949, 1964) defined the numerical response as the change in the number of predators occurring (through immigration or aggregation and reproduction) in response to a prey density. This may further be simplified as the rate of increase in oviposition of predators with an increase in prey density. Thus, numerical response is an important critical tool in determining the nature of interactions between the prey and the predator species, where the former affects the reproduction of the latter (Vieira *et al.*, 2012). This may be through predators' aggregation in prey hotspots or an increase in predator's reproduction and survival.

Mechanism of numerical recruitment driven by immigration of predators is referred to as *aggregative numerical response*; whereas numerical recruitment driven by increased reproduction of predator is referred to as *reproductive numerical response* (Vieira *et al.*, 2012). Factors like attack strategies of predators and the quality of prey species affect the numerical responses (Hemptinne *et al.*, 1992; Palmer & Sheppard, 2002). The oviposition by ladybirds in laboratory conditions may also be influenced by the health and density of the prey (Butin *et al.*, 2003). Moreover, cyclicity and variability in prey dynamics are known to strengthen the numerical response of predators. Since in nature, predators are known to perform both functionally and numerically towards their prey population, but functional response is known to be the key factor as it is thought to be the determinant of numerical response (Keith *et al.*, 1977). Therefore, functional and numerical responses of predators towards changing densities of prey populations are the characteristics to evaluate the suitability of predators as biological control agents.

2.2. Effects on life attributes : The quantity of prey intake, its digestibility and utilisation significantly influence the growth, developmental time, final body biomass and survivability of ladybirds (Rath, 2010). Under prey scarce conditions, cannibalism and intraguild predation (IGP) are important mechanisms that influence the intra- and inter-specific relationships of ladybirds (Sato *et al.*, 2009a,b; Kumar *et al.*, 2014b; Ducatti *et al.*, 2017; Rocca *et al.*, 2017; Yang *et al.*, 2017). Atlihan & Guldal (2009) found increased prey consumption by the ladybird, *Scymnus subvillosus* (Goeze) with an increase in prey density. Similar results were obtained by Britto *et al.* (2009) in ladybird, *Stethorus tridens,* Gordon & Reis *et al.* (2007) in predaceous mite, *Amblyseius herbicolus* (Chant) when fed on tomato red spider mite (*Tetranychus evansi*) and false spider mite (*Brevipalpus phoenicis*), respectively. Increased prey consumption by ladybirds with an increase in prey density has also been reported earlier by Omkar & Srivastava (2001, 2003), Omkar & James (2003), Jalali & Ziaaddini (2017) and Rahimi *et al*. (2017).

Larvae of *H. axyridis* compensated for early prey shortage by accelerating their growth rates (Dmitriew & Rowe, 2007). Similarly, adults of *H. axyridis* had reduced efficiencies in converting prey biomassto egg biomass on limited prey supply than when provided with abundant prey (Agarwala *et al.*, 2008). However, Schuder *et al.* (2004) reported that reduced prey supply slowed down development at all life stages. However, larvae compensated for low prey availability by reducing their development rates, but enhancing their prey exploitation efficiencies, reaching up to 100%, and by increasing prey-

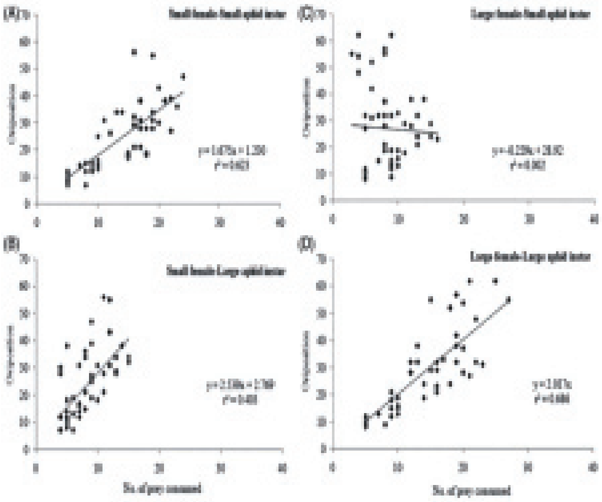
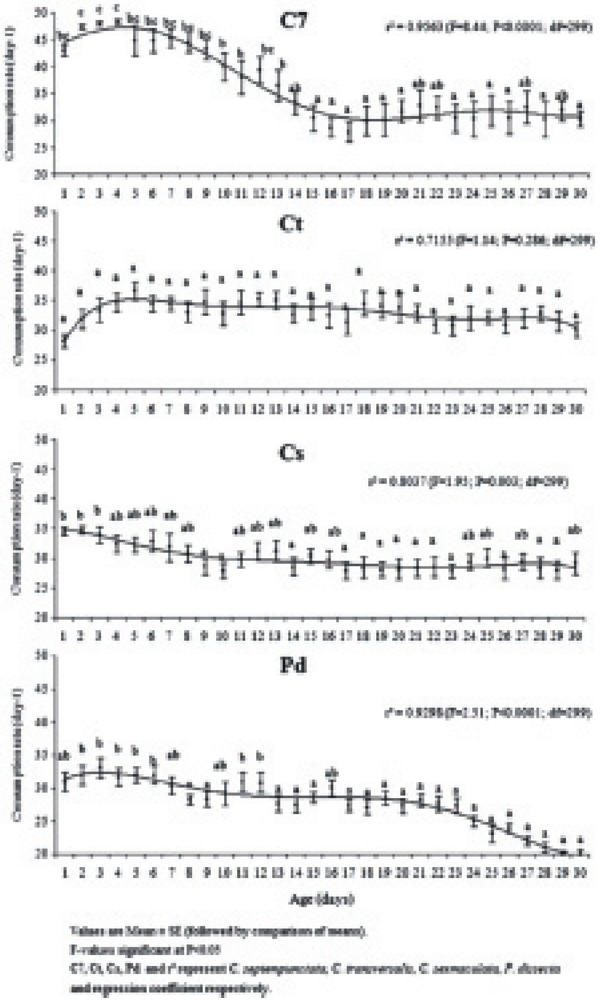


Fig.5. Relationship between oviposition by small and large females of *M. sexmaculatus* and the number of small and large prey instars consumed by them (see Chaudhary *et al*., 2015).



Values are Mean ± SE (followed by comparison of means).
F-values significant at P<0.05
C7, Ct, Cs, Pd and r^2 represent *C. septempunctata, C. transversalis, C. sexmaculata, P. dissecta* and regression coefficient respectively.

Fig.6. Age dependent prey consumption by females of *C. septempunctata* (C7), *C. transversalis* (Ct), *M. sexmaculatus* (Cs) and *P. dissecta* (Pd) on pea aphid (see Mishra *et al*., 2012a).

biomass conversion efficiencies, reaching over 40%. Similar increased rates of ECI (efficiency of conversion of ingested material, *i.e.* percentage of consumed prey biomass converted into predator biomass) at low levels of prey consumption were found in aphidophagous mirids and chrysopids (Zheng *et al.*, 1993a,b).Thus, it appears that the prey biomass conversion rate or ECI varies with prey availability so as to overcome the adverse effects of prey scarcity (Smith, 1965; Waldbauer, 1968; Bista & Omkar, 2014).

Studies have further shown that the reduced rates of prey consumption result in slower development and greater mortality for both the larvae and adults (Phoofolo *et al.*, 2008; Bista & Omkar, 2014). Phoofolo *et al.* (2007) reared larvae of *Hippodamia convergens* Guérin-Méneville on *ad libitum* versus limited quantities (4 mg per day) of *Schizaphis graminum* Rondani and *Rhopalosiphum padi* (L.), both the aphids from winter wheat (*Triticum aestivum* L.). The larvae grew at the same rates on *ad libitum* diets of the two aphid species, but the development of fourth instars was relatively slow on limited diets of *R. padi* and *S. graminum*. Dmitriew & Rowe (2007) investigated the lifetime consequences and compensatory abilities of *H. axyridis* larvae in response to temporary prey shortage during development. Temporary prey shortage and compensatory larval responses thereafter resulted in a lower lifetime fitness cost in terms of a prolonged larval period, greater larval mortality and more rapid death when prey was removed 100 days after experimental subjects reached adulthood.

Prey deprivation severely affects the development and survival of ladybirds (Agarwala *et al.,* 2001; Omkar & Pervez, 2003; Schuder *et al.,* 2004). It is believed that under prey scarce conditions, the entire energy resources are utilised to maximise survival and reproduction (Legaspi & Legaspi, 1998). Thus, prey scarcity can affect the fitness of adults by influencing developmental rate and final size of offspring (Agarwala *et al.*, 2001; Seagraves, 2009). While evaluating the developmental time and survival of *S. subvillosus* at different prey densities, Atlihan & Guldal (2009) found that increased prey density reduced the developmental time and mortality rate. The developmental durations of larval instars of *C. septempunctata* and *C. transversalis* were short, and their larvae pupated earlier when the prey was present in abundance (Maurice & Kumar, 2011).

Agarwala *et al.* (2008), while studying the larval and adult performance of *H. axyridis* on abundant and limited prey availability, reported that under limited prey supply, larvae grew slowly and the surviving adults were small. While studying the intra- and inter-specific interactions on the larval survival of two aphidophagous ladybirds, *C. septempunctata brucki* and *H. axyridis* at two prey densities, Sato *et al.* (2009) concluded that during single species rearing, the number of larvae of both species decreased mainly due to cannibalism. When prey was abundant, the survival of both species improved. In addition, when prey was scarce, cannibalism and IGP became more important factors in intra- and inter-specific relationships of these species (Rocca *et al*., 2017). Recent studies have further shown that at prey abundance the intensity of both intra- and interspecific competitions is low and does not limit predation rates, even for functionally similar predators (Casula *et al.*, 2006). Conversely, when prey is scarce, competition may be stronger (Yang *et al.*, 2017; Ducatti *et al*., 2017), particularly among functionally similar predators (Casula *et al.*, 2006), and in such a case, functionally diverse predators consume more prey (Werling *et al.*, 2012).

Individuals that acquire abundant food from a resource rich environment may be benefitted by transferring their resources to their offspring, thus enhancing their progeny fitness (Qvarnstrom & Price, 2001; Bonduriansky & Head, 2007). However, under low prey consumption females invest less in egg production (Evans, 2003). Studies on *Cingula trifaciata* and *Cingula californica* revealed that females produced eggs in constant ratio to the amount of food available to them (Ives, 1981). Females invest a limited degree in egg production even in absence of aphid prey to enhance their ability to oviposit quickly upon locating patches of high aphid density (Evans, 2000). It appears that females use the resources from limited prey consumption to support modest egg production. Engelmann (1970) stated that the number of ovarioles per ovary is reduced when the supply of food during the larval stage is limited. During the time of food scarcity, many species utilize their energy reserves to maintain survival. Under these circumstances, the cost of maintaining normal metabolic processes of the organism is depletion of fat reserves. However, the way to reduce this cost is to lower fecundity and use the scant energy available for keeping itself alive (Ricklefs, 1990).

Although, the clutch size and oviposition rates are influenced by the prey quantity available to females at the time of oviposition (Dixon & Guo, 1993; Dixon, 2000; Ware *et al.,* 2008), the prey availability during immature growth and development is much important even when adult diet is optimal. However, the development of offspring is influenced by both the nutrient reserves in eggs and the food provided to them during development (Bertram & Strathmann, 1998). Dixon & Guo (1993) suggested that this is due to the effect of larval prey supply on adult size and ovariole number. Agarwala *et al*. (2009) reported that females of *Harmonia dimidiata* (F.) matured earlier and

Table 3: Effect of quality of prey on reproductive attributes of *C. septempunctata* (C7) and *C. transversalis* (Ct) (see Bista and Omkar, 2014)

Ladybird species	Pre quantity	Pre-oviposition period (days)	Oviposition period (days)	Post oviposition period (days)	Fecundity (No. of eggs)	Egg fertility(%)	Female longevity (days)	Male longevity (days)
C7	Low	19.00±0.60^{c}	40.30±0.52^{a}	10.40±0.54^{a}	784.90±30.15^{a}	81.23±1.34^{a}	69.70±2.07^{a}	64.90±1.45^{a}
	Medium	12.50±0.43^{b}	52.70±1.12^{b}	11.90±0.64^{a}	1439.90±44.20^{b}	87.17±0.94^{b}	11.10±2.26^{b}	70.50±1.88^{ab}
	High	11.30±0.65^{a}	54.50±0.50^{c}	11.80±0.49^{a}	1546.60±41.61^{c}	89.17±0.98^{c}	77.60±1.23^{b}	71.10±1.46^{b}
Ct	Low	9.20±0.13^{c}	38.50±0.54^{a}	11.10±0.41^{a}	794.60±30.84^{a}	82.72±0.67^{a}	58.80±1.60^{a}	56.20±1.75^{a}
	Medium	7.00±0.26^{b}	52.70±0.84^{b}	10.10±0.53^{a}	1561.30±44.91^{b}	89.87±0.87^{b}	69.80±1.26^{b}	64.20±1.58^{b}
	High	6.40±0.16^{a}	55.10±0.72^{c}	8.80±0.33^{a}	1604.10±45.61^{b}	90.82±0.80^{b}	70.30±1.30^{b}	65.80±1.48^{b}
Ladybird species		*F*=380.16 *P*<0.0001 df=1,59	*F*=0.44 *P*=0.511 df=1,59	*F*=11.27 *P*=0.001 df=1,59	*F*=3.65 *P*=0.061 df=1,59	*F*=6.20 *P*=0.016 df=1,59	*F*=11.19 *P*=0.001 df=1,59	*F*=2.20 *P*=0.144 df=1,59
Prey quantity		*F*=88.13 *P*<0.0001 df=2,59	*F*=254.30 *P*=0.0001 df=2,59	*F*=1.01 *P*=0.370 df=2,59	*F*=231.57 *P*=0.0001 df=2,59	*F*=38.81 *P*=0.0001 df=2,59	*F*=444.41 *P*=0.0001 df=2,59	*F*=486.00 *P*=0.0001 df=2,59
Interaction		*F*=19.97 *P*<0.0001 df=2,59	*F*=1.42 *P*=0.250 df=2,59	*F*=7.16 *P*=0.002 df=2,59	*F*=0.97 *P*=0.387 df=2,59	*F*=0.21 *P*=0.810 df=2,59	*F*=38.71 *P*=0.0001 df=2,59	*F*=53.03 *P*=0.0001 df=2,59

Values are means ± SE

Small letters represent comparison of means among prey quantities within each ladybird species

produced more eggs at high prey (*Cervaphis quercus* Takahashi) density, while at low prey density the females matured late and either did not produce eggs or produced fewer eggs. While studying the larval and adult performance of *H. axyridis* on abundant and limited food availability, Agarwala *et al*. (2008) reported that under limited food conditions the larvae grew slowly, surviving adults were small with prolonged pre-reproductive periods and reducedfecundity, but had increased longevity than those reared under abundant food conditions.

Because the quantity of prey consumed affects development, survival and reproduction of predators (e.g. Zheng *et al.,* 1993a,b; Dmitriew & Rowe, 2011; Bista & Omkar, 2014), one must study predators' responses to prey availability for understanding their ecology, foraging efficiency and rate of prey consumption. Since performances of both larval and adult predators are constrained by the quantity of prey available (Hodek & Honek, 1996; Lee & Kang, 2004; Seagraves, 2009; Bista & Omkar, 2014), the factor is very important in understanding the fate of predatory insects. Moreover, how prey availability impacts female ladybirds in terms of their size and age at maturity and how these, in turn, affect fecundity, are also important in understanding the ecology and potential of ladybird predators for their use in biocontrol programs against insect pests (Agarwala & Bhowmik, 2011).

3. Mobility and defence of prey

Prey mobility is another factor that influences prey selection by ladybird predators. Several studies have demonstrated that prey mobility increases the prey searching and handling time by predators that results in a reduced net energetic gain (e.g., Allan *et al.*, 1987; Nordlund & Morrison, 1990). However, Rosenheim & Corbett (2003) have demonstrated that for a sit and-wait predator, high prey mobility could increase encounter rate and attack probability. The selection of prey by ladybird predatorsis greatly affected by prey activity (Provost *et al*., 2006). Ladybirds generally attack only the most vulnerable preyin presence of active prey, but select preferentially active preyin presence of immobilized individuals. Provost *et al*. (2006) have further reported that in presence of active prey, ladybird *H. axyridis* was unable to capture the mirid prey, *Hyaliodes vitripennis* (Say) because the prey was highly mobile and used effective defensive mechanisms to escape the attacks.

In addition, several studies have demonstrated that mobile prey generally increase foraging costs, reduce probability of capture and result in a lower net energetic gain for the predator (*e.g.* Allan *et al.*, 1987; Nordlund & Morrison, 1990). Prey defensive mechanisms could also influence prey selection. Roger *et al.* (2000) observed a reduced capture rate of prey with effective defensive responses by the ladybird, *Coleomegilla maculata*

(DeGeer). In contrast, Soares *et al.* (2004) observed that distribution and defensive strategies of prey species, *M. persicae* and *A.fabae* did not provide any escape advantage from the ladybird, *H. axyridis aulica*. Similarly, Kumar *et al.* (2014b) reported that the immobility and defensive surface semiochemicals of conspecific and heterospecific eggs, rich in alkanes and alkaloids (Hemptinne *et al*., 2000a,b; Omkar *et al*., 2004), reduced their consumption and utilization by the larvae of *C. septempunctata* and *C. transversalis*.

It is further believed that the least suitable prey sequesters chemicals from their host plants, which contain certain alkaloids that are toxic for many ladybirds (Hodek, 1956; Okamoto, 1966). For example, the pungent smell of mustard aphid is possibly due to the presence of allyl isothiocyanates, and is responsible for its reduced suitability as a prey (Joshi *et al*., 1999; Noble *et al*., 2002; Omkar *et al*., 2009a). There are also possibilities that the allelochemicals that the mustard aphid derives from its host plant may not be detoxified by many ladybird predators causing its lower patatibility (Kumar *et al*., 2013).

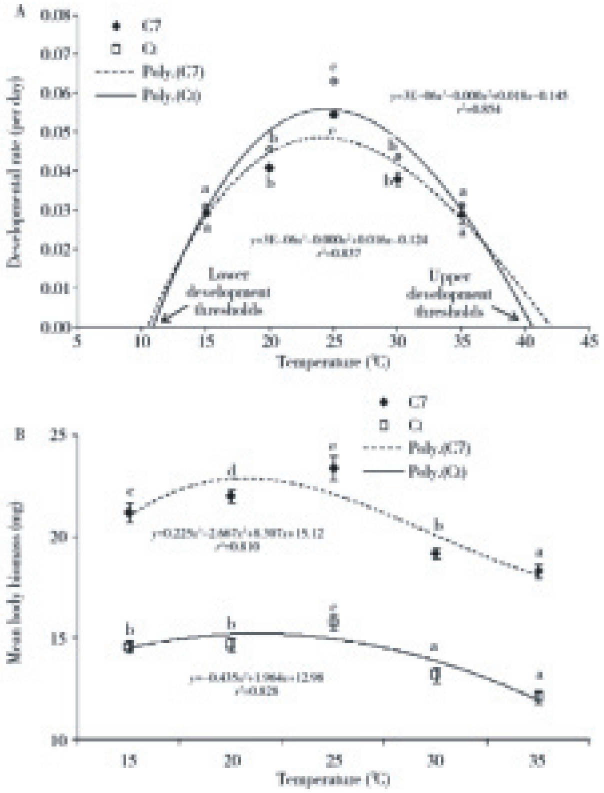


Fig.7. Effect of temperature on developmental rate of larvae and mean body biomass of newly emerged adults of *C. septempunctata* (C7) and *C. transversalis* (Ct) (see Omkar and Kumar, 2016)

While *A. craccivora* has high suitability and palatability for *C. septempunctata* (Omkar & Srivastava, 2004a), *C. transversalis* (Bista & Omkar, 2013; Kumar *et al*., 2013); *M. sexmaculatus* (Omkar & Bind, 2004; Kumar *et al*., 2013; Patel *et al*., 2017) and *P. dissecta* (Omkar & Mishra, 2005; Kumar *et al*., 2013) when reared on bean (*D. lablab* Linnaeus; Fabaceae). However, *A. craccivora* obtained from host plants such as *Robinia pseudoacacia* L. (Fabaceae) (Obatake & Suzuki, 1985), *Astragalus sinicus* L. (Fabaceae), *Vicia hirsuta* (L.) (Fabaceae), *Capsella bursa-pastoris* (L.) (Brassicaceae), *Cardamine flexuosa* With. (Brassicaceae), *Rorippa palustris* (L.) (Brassicaceae) and *Hemistepta carthamoides* Kuntze (Asteraceae) (Hukusima & Kamei, 1970) have been reported to be highly toxic to ladybirds, probably due to the presence of amines, canavanine and ethanolamine, from both the host plants and the aphid species (Obatake & Suzuki, 1985).

4. Morphology,age and parasitisation status of prey

Prey size significantly influences the prey selection by ladybird predators. Previous studies have correlated the prey size with nutrient gain, *i.e.* a large prey provides higher energetic gain to predators than a small prey (Roger *et al*., 2000; Sloggett, 2008a,b; Skelhorn & Rowe, 2006; Skelhorn *et al*., 2016). Houck (1991) demonstrated that the ladybird, *Stethorus punctum* (LeConte), selected its prey according to prey quality and nutritional needs. *Homalodisca vitripennis* is a larger prey than *Tetranychus urticae* Koch, and the prey quality experiment demonstrated that when considering only nutrient content, *H. vitripennis* provided a faster development for *H. axyridis* larvae with a lower mortality rate than *T. urticae* (Provost *et al*., 2006). While a larger prey can supply higher nutrients, the attack and capture of larger prey could be more expensive and risky (Allan *et al*., 1987; Roger *et al*., 2000).

Harmon *et al*. (1998) measured the foraging ability of *C. septempunctata*, *H. axyridis*, *H. convergens* and *C. maculata* on red and green colour morphs of the pea aphid on red, green, and white backgrounds. They reported that *C. septempunctata* consumed significantly more of the aphid morph that contrasted with the background colour, and showed no difference between morphs on the white background. However, *H. axyridis* consumed significantly more numbers of red morph aphids regardless of background. The remaining two species showed no difference in consumption rates on the two colour morphs. The variation in the use of visual cues thus demonstrates that different species of predators can exhibit different for aging behaviour when searching for the same prey.

Prey age also influences the feeding behaviour of predators. Zarghami *et al*. (2014) examined the feeding

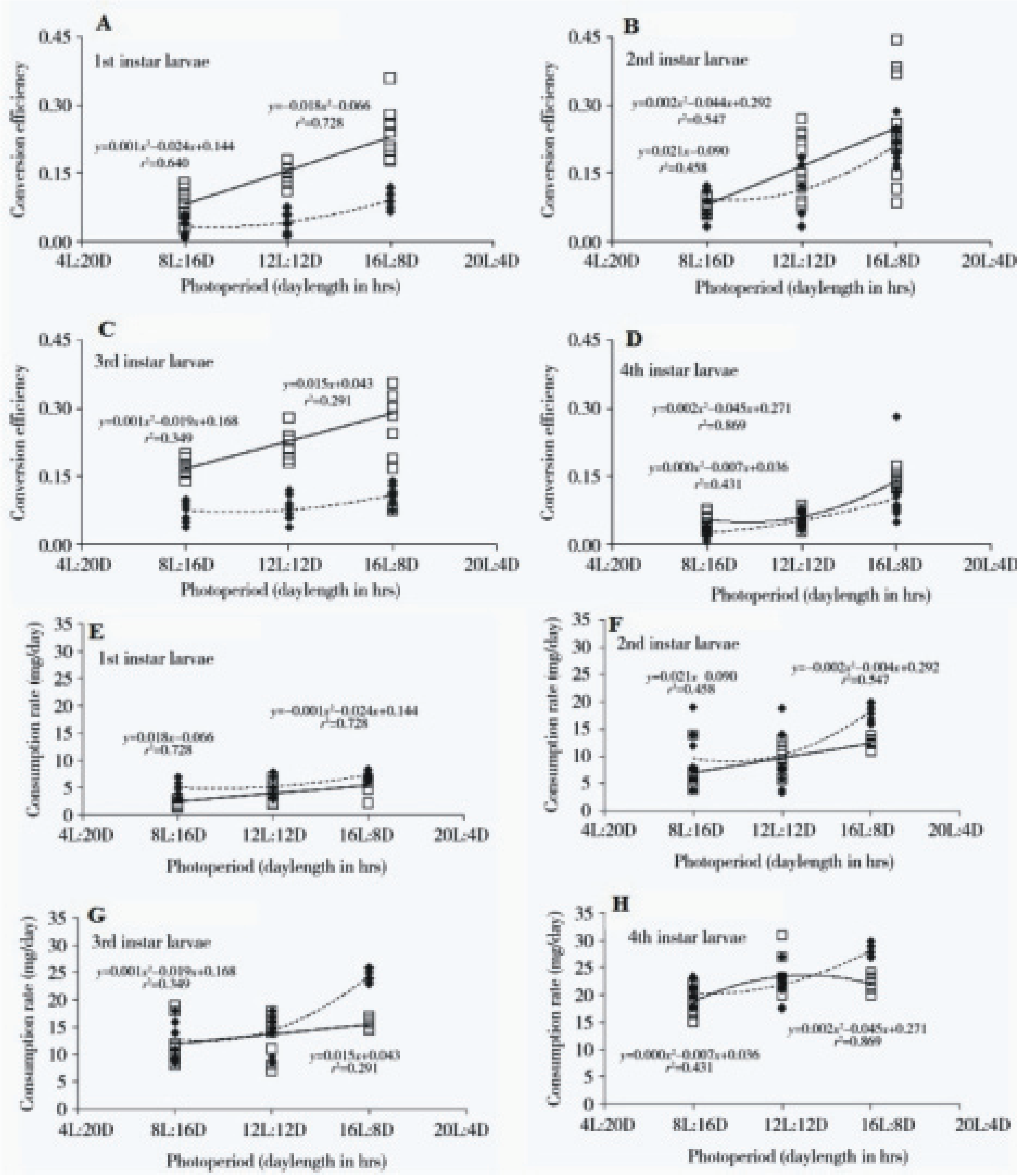


Fig. 8. Effect of photoperiod on predation attributes of *C. septempunctata* (C7) and *C. transversalis* (Ct) larvae (see Omkar and Kumar, 2016).

habits of the coccidophagous ladybird, *Nephus arcuatus* Kapur, on two mealybugs, *Nipaecoccus viridis* (Newstead) and *Planococcus citri* Risso; and reported that *N. arcuatus* consumed significantly more number of first-instar nymphs than the eggs, and more eggs than the adult females of both the prey species. There are also reports indicating that ladybirds discriminate their prey, based on the parasitisation status of the prey (Al-Zyoud & Sengonca, 2004). Discrimination could be based either on physical changes in the prey after parasitisation or on the presence of external or internal marking left by the female parasitoid during or after oviposition (van Baaren *et al*., 1995).

The larvae of the ladybird, *C. maculata*, are able to discriminate between eggs of *Trichoplusia ni* (Hubner) (Lepidoptera: Noctuidae) of different quality. Eggs that are parasitized by *Trichogramma turkestanica* Meyer (Hymenoptera: Trichogrammatidae) gradually decrease in quality and are less accepted by *C. maculata* larvae towards the end of parasitoid immature development (Roger *et al*., 2001; Al-Zyoud & Sengonca, 2004). Thus, *C. maculata* larvae prefer young eggs as their prey; however, pre-imaginal developmental time and food intake to reach adulthood increase and survival decreases when *C. maculata* larvae are fed with old parasitized eggs rather than with young unparasitized eggs (Roger *et al*., 2001; Al-Zyoud & Sengonca, 2004). Thus, while developing biocontrol strategies against agricultural pests, size, age, and parasitisation status of pest species need to be assessed so as to execute the proposed biocontrol strategies successfully.

5. Size, stage, sex and age of predator

In an agroecosystem, ladybird predators partition their prey on the basis of their own size and the size of their prey. When kept together, the predators of small and large size capture and consume smaller and larger prey, respectively (Stephens & Krebs, 1986; Sloggett, 2008a,b; Costa, 2009). Optimal foraging models also predict that large predators should prey upon large prey to maximise their energy intake (Stephens & Krebs, 1986). Apart from the body size, resource partitioning by ladybird beetles is also governed by the prey density. Small ladybird species have low energy requirements; they therefore feed on low densities of smaller prey. In contrast, they require high densities of larger prey having sufficient numbers of smaller instars (Dixon, 2007). However, the low densities of smaller prey cannot fulfill the high energy requirements of large ladybird species that require either: (i) high densities of smaller prey, or (ii) low densities of larger prey, at which they can easily capture even the biggest prey instars, which are of greater energy sources than the smaller ones (Dixon, 2007; Sloggett, 2008a, b) (Fig. 5).

Chaudhary *et al*. (2015) revealed that under the choice condition, small and large females of *M. sexmaculatus* consumed a higher number of smaller and larger prey instars, respectively. However, small females exhibited a modified Type II functional response on smaller prey instars and a Type II functional response on larger prey instars. Contrary to them, the large females exhibited a Type II functional response when provided either smaller or larger prey instars. Further, in small females, oviposition was positively correlated with the numbers of smaller and larger prey instars consumed, being stronger for the smaller prey instars. In large females, oviposition was positively correlated with the numbers of larger prey instars consumed and not by the smaller prey instars.Thus, prey abundant conditions are better exploited by large ladybirds while small ladybirds are more effective in exploiting the prey under scarce prey conditions (Dixon, 2007; Sloggett, 2008a,b). Studies have further revealed that prey colonies are often first attacked by a small and then a large species of ladybird, and the smaller species starts exploiting the prey resource before the larger species (Dixon, 2007; Sloggett, 2008a,b), indicating the former to be more effective during exploitative competition (Omkar *et al*., 2014). Therefore, the abundance or scarcity of prey governs the coexistence of ladybirds within an agroecosystem.

Prey preference in ladybirds may also be affected by the stage, sex and age of predators (Fig. 6; Table 4). Numerous studies have exemplified that in ladybirds, the fourth instars have higher prey consumption rates than the early instars. In contrast, the early instars have higher prey conversion efficiencies and growth rates than the fourth instars (Mishra *et al*., 2011, 2012a; Omkar *et al*., 2014; Kumar *et al*., 2014b). The higher prey consumption by fourth instars and adult females over the males has also been reported earlier (Omkar & Srivastava, 2001; Mishra *et al*., 2011, 2012a; Kumar *et al*., 2013).While evaluating the prey preference (*A. gossypii*) of larvae and adults of *C. transversalis* and *M.sexmaculatus*, Veeravel & Baskaran (1995) observed that only the larval stages showed preference for the prey species and not the adult stages. However, Soares *et al*. (2004) observed that the prey preference of adult *H. axyridis aulica* differed between genders; no feeding preference was observed for the females in the presence of both *M.persicae* and *A. fabae*, while males showed a preference for *M. persicae*. The authors suggested that *H. axyridis* females presented self-selection behaviour, but prey preference in males was correlated with prey size. While assessing the feeding habits of the ladybird, *N. arcuatus*, the consumption capacity of males and females was determined by feeding on eggs, first-instar nymphs, and adult females of the two

Table 4: Stage specific prey consumption by larvae of *C. septempunctata* (C7), *C. transversalis* (Ct), *M. sexmaculatus* (Cs) and *P. dissecta* (Pd) on pea aphid (see Mishra *et al.,* 2012a)

Species	Stages	Conversion efficiency	Relative growth rate (mg/days)
C. septempunctata (C7)	First instar	0.09±0.006^{c}	0.77±0.059^{b}
	Second instar	0.21±0.012^{c}	1.17±0.036^{c}
	Third instar	0.11±0.006^{a}	0.61±0.064^{b}
	Fourth instar	0.14±0.005^{b}	0.40±0.020^{a}
C. transversalis (Ct)	First instar	0.09±0.010^{a}	0.59±0.083^{b}
	Second instar	0.25±0.038^{b}	1.25±0.119^{c}
	Third instar	0.30±0.043^{b}	0.73±0.127^{b}
	Fourth instar	0.10±0.021^{c}	0.21±0.015^{a}
C. sexmaculata (Cs)	First instar	0.34±0.030^{c}	2.10±0.159^{c}
	Second instar	0.22±0.022^{ab}	0.80±0.093^{b}
	Third instar	0.24±0.017^{b}	0.65±0.046^{b}
	Fourth instar	0.17±0.007^{a}	0.33±0.018^{a}
P. dissecta (Pd)	First instar	0.28±0.028^{b}	1.07±0.071^{b}
	Second instar	0.20±0.018^{ab}	0.38±0.046^{a}
	Third instar	0.29±0.075^{b}	0.56±0.108^{a}
	Fourth instar	0.13±0.015^{a}	0.48±0.078^{a}
Species (C7, Ct, Cs, Pd)	*F*-value (*P*-value); DF	10.41 (<0.0001); 3, 159	13.39 (<0.0001); 3, 159
Stage (L1, L2, L3, L4)	*F*-value (*P*-value); DF	9.26 (<0.0001); 3, 159	66.60 (<0.0001); 3, 159
Interaction	*F*-value (*P*-value); DF	7.07 (<0.0001); 9, 159	26.86 (<0.0001); 9, 159

Note: Values are means ± SE; *F*-value significant at $P<0.05$; superscript letters represent comparison of means between stages within each species; same letters indicate values tobe statistically similar

mealybugs, *N.viridis* and *P. citri* (Zarghami*et al*., 2014). It was reported that the prey preference of females did not change with the developmental stage of the mealybug. However, males reared on either *N. viridis* or *P. citri* showed a significant preference for the first-instar nymphs of *P. citri* over those of *N. viridis*.

Further, a decline in prey consumption and rate of assimilation in ladybirds with an increase in age has also been reported (Veeravel & Baskaran, 1995; Dixon & Agarwala, 2002). Mishra *et al*. (2012a) evaluated stage- and age-specific predatory patterns and nutritional ecology attributes of four co-occurring aphidophagous ladybirds, namely, *C. septempunctata*, *C. transversalis*, *M. sexmaculatus* and *P. dissecta* on pea aphid. It was found that despite having lower consumption rates, small ladybirds (*M. sexmaculatus* and *P. dissecta*) and their early larval instars were efficient converters of prey with higher relative growth rates than the large ladybirds (*C. septempunctata* and *C. transversalis*) and their late instars. In addition, the consumption of prey by ladybird larvae increased with age, but with a slight decline in prey consumption just prior to pupation. Moreover, adult females of early age groups had higher consumption rates than later age groups in all the four ladybird species, and the consumption rates of adult females further decreased with an increase in their age.

Bista & Omkar (2014) also reported similar results while assessing the predation and reproductive attributes of *C. septempunctata* and *C. transversalis* under low, medium and high prey biomasses. In their study, females of both the ladybird species exhibited triangular fecundity and egg fertility functions and plateau shaped prey consumption rate function with age, indicating towards their highest reproductive performance during middle age on the three prey biomasses; being highest on high prey biomass. However, on the three prey biomasses, females had higher body biomass conversion efficiency during pre- and post-oviposition periods and higher egg biomass conversion efficiency during the oviposition period; being highest on high prey biomass. They further concluded that middle aged ladybirds reared on high prey biomass might suppress pest populations better than those reared on low/medium prey biomass. Thus, it is advisable to consider the above parameters as good indicators for identification of the most suitable ladybird species for their mass multiplication in laboratories for augmentative biocontrol programs.

6. Learning ability and memory of predator

Insect predators respond to diverse external cues while in search of food, shelter, oviposition sites or the mates (Dukas, 2008). While most of these cues are innate, some may be learned during the predator's lifetime (Remen, 2004; Giurfa, 2013,2015). Further, if learned information is integrated into the prey searching process, the rate of encountering herbivore pests by these predators may be increased (Papaj, 1993). Optimal foraging models predict that a foraging predator has to maximise its encounter rate with the most suitable and profitable prey and avoid lesser quality resource items (Stephens & Krebs, 1986). However, for generalist predatory insects that can be exposed during successive generations to different prey species living in various microhabitats, recognition of specific cues to identify the most suitable prey is unlikely (Papaj, 1993; Hirvonen *et al*., 1999). Under such conditions, learning, (*i.e.* a gradual change in behaviour following continued experience and which can be forgotten with time; van Baaren & Boivin, 1998), may be adaptive because it allows an individual to acquire neuronal representations of spatial environmental configurations, sensory information or associations between perceived stimuli and environmental states (Dukas, 2008) and to adapt to a variety of situations that may be encountered (Lewis *et al*., 1990).

Predaceous ladybirds use olfactory and visual cues to detect resource-rich habitats and, with experience, they learn to associate these cues with the most profitable habitats containing suitable prey (Remen, 2004; Perez-Maluf *et al*., 2008; Hodek *et al*., 2012; Rondoni *et al*., 2017). Thus, learning is likely to be an important capability to increase the overall foraging efficiency of ladybirds. Studies have further shown that the pre-imaginal and adult learning is widespread among phytophagous insects (Dukas & Bernays, 2000; Xue *et al*., 2007), parasitoids (Stireman, 2002; van Baaren *et al*., 2005; Dauphin *et al*., 2009), and social insects (Farina *et al*., 2005). However, the adaptive value of learning in prey selection by ladybird predators has received little attention (Biovin *et al*., 2010; Hodek *et al*., 2012).

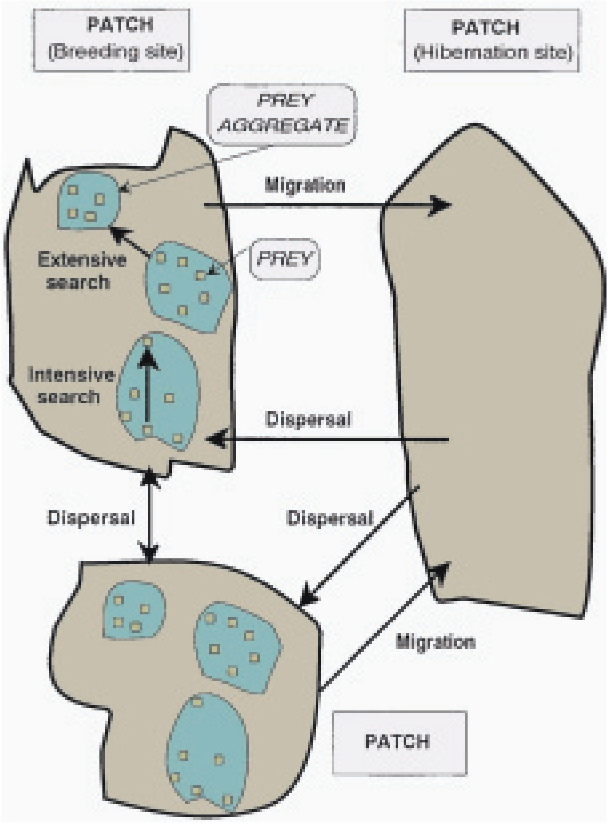


Fig.9. Assessment of prey patch by ladybirds and the foraging behaviour displayed by them (see Ferran & Dixon, 1993)

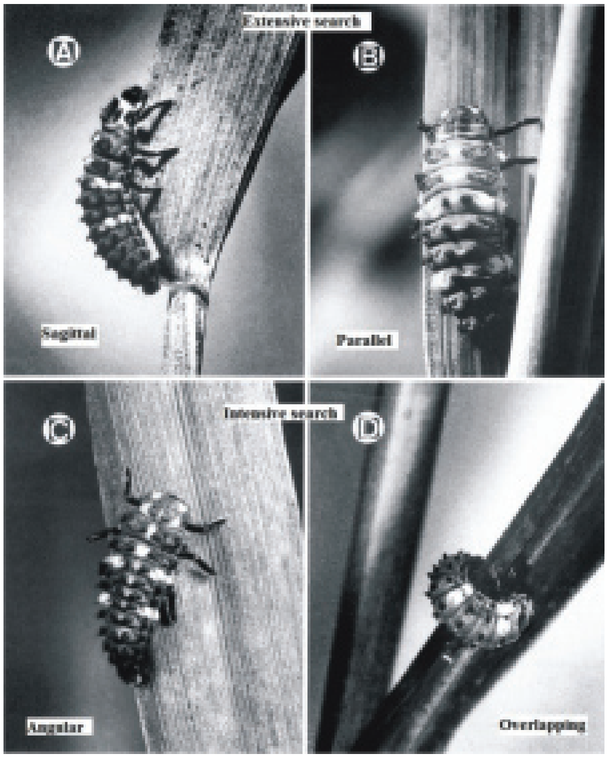


Fig.10. Various positions taken by *C. septempunctata* larva during extensive (*i.e.* (A)-Sagittal; (B)-Parallel) and intensive (*i.e.* (C) Angular; (D) Overlapping) search (see Ferran & Dixon, 1993)

Numerous studies have reported an improvement in searching behaviour (Ettifouri & Ferran, 1993), capture efficiency (Guillette *et al*., 2009), and prey recognition in adult predators (Guershon & Gerling, 2006) due to previous experiences (Dejean *et al*., 2003). Papaj & Prokopy (1989) have proposed that learning occurs when an individual's behaviour: (1) changes in a repeatable way as a consequence of experience, (2) changes gradually with continued experience, and (3) vanishes in the absence of continued experience of the same type, or as a consequence of a novel experience or trauma (Biovin *et al*., 2010). Thus, the evolution of learning depends on the predictability of the environment within or between generations (Boivin *et al*., 2004), but learning is more likely to occur when the environment changes between generations but remains constant within a generation (Stephens, 1991).

It has been demonstrated in insects that the physiological state and previous oviposition experience could influence their learning rate (van Baaren *et al*., 2005) and preference (Bjorksten & Hoffmann, 1995). In their study, Biovin *et al*. (2010) reported that hunger and experience with other food types had little effect on the rate of learning but rather changed the initial level of rejection of low-quality prey. Thus, the initial level of rejection of low-quality eggs was higher in *Coleomegilla maculata lengi* Timberlake (Coccinellidae) larvae previously fed with aphids than in starved larvae, but the opposite was obtained when larvae were previously fed with low-quality eggs. These results further indicate that previous experience might alter the preference of prey types and consequently may affect the selection of resource items and the patch exploitation strategy (Vet *et al*., 1990; van Baaren *et al*., 2005). Moreover, through experience, larvae can select their resource more effectively in mixed patches of prey and learning may further improve their overall foraging efficiency (Punzo and Garman, 1989; Papaj and Vet, 1990; Johnson, 1991; Biovin*et al*., 2010).

7. Environmental factors

The environment around every organism is composed of various abiotic and biotic factors. Among these, temperature and photoperiod are the crucial climatic factors that directly affect the population of insect pests and their natural enemies, *viz*. the ladybird beetles (Pervez & Omkar, 2004b; Omkar *et al*., 2009b; Dell *et al*., 2013; Kumar & Omkar, 2015; Omkar & Kumar, 2016; Morales-Ramos & Rojas, 2017).

7.1. Temperature : Temperature extremes limit the geographic range of insect populations, either causing direct mortality or limiting the range of host plants or animals. Both the insect predators and pests, being poikilothermic in nature, are significantly influenced by temperature.Temperature influences their various biological characteristics, *viz.* development, survival, adult longevity, fecundity and fertility (Omkar & James, 2004b; Pervez & Omkar, 2004b; Omkar *et al*., 2008, 2009; Ramalho *et al.,* 2009; Regniere *et al.*, 2012; Majumder & Agarwala, 2013; Jarosik *et al*., 2013; Omkar & Kumar, 2016; Morales-Ramos & Rojas, 2017). Studies have revealed that increase in environmental temperature increases the metabolic rates of insects that further enhance their rates of prey consumption (Ba M'Hamed & Chemseddine, 2001). However, insects avoid low temperature extremes by migration and dispersal or diapause. Fitness also decreases as temperature increases above the optimum (Denis *et al.*, 2011). Thus, temperature sets the limits of performance of insects in terms of low and high thermal thresholds, and these thresholds are the major determinants of their various life processes.

The developmental (Perdikis & Lykouressis, 2002) and food consumption (Anderson *et al.,* 2001) rates of insects generally increase with increase in temperature (Kumar & Omkar, 2015; Omkar & Kumar, 2016). Rate of metabolism also varies with temperature (Sentis *et al.*, 2012). Studies have shown that the predation rate, which is a modified Holling's type II functional response, is temperature dependent and temperature influences the predator's time to search, capture and handle the prey (Gillooly *et al.*, 2002; Rahimi *et al*., 2017). Low temperature slows down the development and increases the length of periods in various life stages of insects. Strong variations in daily temperature amplitude may mean that insects cannot meet their nutritional needs, leading to their higher mortality. On the other hand, increased temperature could diminish the effects of low food quality (Wolesensky *et al.*, 2005). Studies have further shown that the influence of temperature on prey consumption rate differs from species to species. Also, a temperature regime suitable for one insect species may be less or unsuitable for the other species (Allawi, 2006).

While studying the effect of temperature on the functional response of adult females of the two-spotted ladybird, *A. bipunctata*, on green-peach aphid, *M. persicae*, Jalali *et al.* (2010) reported that the predator showed a type II functional response at three tested temperatures ranging from19°C to 27°C. The theoretical maximum number of prey captured by the predator increased with an increase in temperature. However, prey handling time significantly decreased as temperature increased from19°C to 27°C.

Depending on the developmental strategy of the ladybird species, temperature can exert different effects (Pervez & Omkar, 2004b). Individuals kept at high temperatures completed their development earlier than those kept at low temperatures (Omkar & Kumar, 2016). However, they all spent the same proportion of the total time required to complete their development per stage. This phenomenon is referred to as 'development rate isomorphy' (Jarosik *et al.*, 2002). In this case, the lower thermal threshold (*i.e.* the temperature below which development does not occur) is uniform in developmental stages within populations and within species (Dixon *et al.,* 1997). While evaluating the predation attributes and developmental rates of two ladybird species, *C. transversalis* and *C. septempunctata*, on pea aphid, Omkar & Kumar (2016) found the attributes to be highest at 25°C than at 15°C, 20°C, 30°C and 35°C. Moreover, non-linear regression models extrapolated as ~11°C and ~10.5°C as lower development thresholds and ~41°C and ~43°C as upper development thresholds for *C. transversalis* and *C. septempunctata*, respectively. From this study, it was further revealed that a ubiquitous ladybird is less susceptible to climatic cues than an indigenous ladybird and is widely distributed to different geographical regions, behaving as a good biocontrol agent (Fig. 7).

It is well known that intraspecific variation in developmental traits, especially under critical temperatures, is very common in ladybirds (Lamana & Miller, 1998). High temperature accelerates the development and causes earlier emergence of larvae from the egg stage (Omkar & James, 2004b; Omkar & Pervez, 2004; Damos & Savopoulou-Soultani, 2012). Temperature variations affect the daily activity periods, causing either the predator or the prey to be more or less active. Therefore, predator search times can be strongly affected by the temperature (Logan *et al.*, 2006).The energy partitioning model further elucidates the impact of temperature and age in shaping the fecundity function in ladybirds (Kindlmann *et al.*, 2001). Temperature driven age-specific fecundity function of ladybirds is triangular in shape, with an initial increase in daily oviposition rate, reaching a peak and thereafter declines with further increase in age (Pervez & Omkar, 2004b). A gradual increase in temperature expedites this peak of oviposition rate towards the younger side of the ageing ladybirds. At optimum temperature, which is almost 27°C-30°C in most aphidophagous ladybirds, the oviposition peak is attained at the youngest age of the ladybird demography (Pervez & Omkar, 2004b). Thereafter, this peak gets delayed and shortened with further rise in temperature.

Increase in temperature also accelerates progeny development and reduces their mortality. This has been well established in *A. bipunctata* larvae feeding on the grain aphid, *Sitobion avenae* (F.) (Schuder *et al.*, 2004). Similarly, durations of all stages of *Stethorus tridens* Gordon decreased with increasing temperature (Fiaboe *et al.*, 2007). Development durations of immature stages of ladybird, *S. subvillosus* reared on plum aphid, *Hyalopterus pruni* (L.), also decreased with an increase in temperature (Atlihan & Chi, 2008). Total developmental duration of *Cs. bipustulatus* reared on oleander scale, *Aspidiotus nerii* Bouché was lowest at 32.5°C and highest at 15°C (Eliopoulos *et al.*, 2010). The survival of immature stages of *P. quatuordecimpunctata* varied significantly across temperatures with the lowest (14%) survival at 32.5°C and highest (96%) at 25°C. In addition, temperature showed a profound effect on female longevity in this viable range of temperatures, as it decreased from 123.06 days at 17°C to 33.53 days at 30°C (Papanikolaou *et al.*, 2013). Both, longevity and feeding rate of females of the ladybird, *M. discolor* was lower at 23.5°C when compared with those reared at 30.71°C (Hong *et al.*, 2013). Khan & Spooner-Hart (2017) studied the influence of temperature on development of ladybird, *Stethorus vagans* Blackburn, fed on *T. urticae* at seven constant (10, 12, 15, 20, 25, 30 and 35°C) and fluctuating (12.7-32.1°C) temperatures; and observed a strong positive correlation between the rate of development and temperature.Thus, it appears that the biocontrol strategy against insect pests would be at threshold levels if prey-predator relationships are established at the optimum temperature range.

7.2. Photoperiod and light intensity : Seasonal activity in insects is usually governed by abiotic factors, and light is the major factor among them that determines the timing of a ladybird's activity synchronized with its environment (Luker *et al.,* 2002; Hao *et al.*, 2013). The duration of light in a day-night cycle (24 h) is termed as photoperiod. Light can be described in terms of its properties of periodicity (seasonal day length changes), quality (*i.e.* spectral profile) and quantity (*i.e.* light intensity) (Downing & Litvak, 2002). These in turn exhibit both spatial and temporal variations among species (Urbanski *et al.*, 2012). Response of insects towards fluctuating photoperiod can be quantitative, but the degree of response is consistent with actual duration of the photoperiod (Zaslavski, 1996). The photoperiod also governs the gross hormonal and gonadal changes necessary for the transition between developmental states and reproductive activity/ inactivity in insects. However, the duration of photoperiod other than above or below the critical length has no influence (Danks, 2007).

Insects predict the future seasonal environmental conditions through alteration in day length. They perceive alteration in photoperiod very efficiently, even when the differences from day to day are relatively small at some times of year and at lower latitudes. Chunju *et al.* (2012) reported that photoperiod, as an ambient environmental factor, was important for the stimulation of alate aphids in

Table 4: Effect of photoperiod and wavelength of light on the predation and reproductive attributes of *C. saucia* (see Omkar & Pathak, 2006)

	Pre-oviposition period (in days)	Fecundity (no. of eggs)	Egg viability (%)	Oviposition at peak (no. of eggs)	Day of peak	Reproductive rate	Fitness	Prey consumption
(a) Photo-periods								
8:16h (L:D)	7.50±0.70^{b}	310.80±67.68^{a}	92.41±3.46^{a}	38.50±5.60^{a}	18.70±5.27^{b}	10.36±2.25^{a}	0.53±0.07^{a}	122.90±4.46^{a}
16:8h (L:D)	6.50±0.52^{a}	784.60±91.73^{c}	97.06±1.06^{c}	51.30±6.03^{b}	8.00±1.16^{a}	26.15±3.05^{c}	0.78±0.09^{c}	147.50±21.00^{b}
24:0h (L:D)	7.20±0.78^{ab}	477.70±35.82^{b}	93.13±4.05^{b}	40.00±9.35^{a}	12.70±8.38^{ab}	15.92±1.19^{b}	0.65±0.11^{b}	139.90±9.42^{b}
F-values	5.64***	121.35***	6.38***	9.45***	8.40***	121.34***	17.17***	8.66***
(b) Wave-length								
White	5.30±0.48^{a}	1044.1±51.2^{d}	95.19±4.27^{a}	50.30±2.21^{c}	13.40±2.63^{a}	3.17±0.14^{b}	0.73±0.06^{c}	166.80±7.63^{b}
Yellow	6.50±0.52^{b}	681.1±52.8^{c}	91.5±4.34^{a}	42.90±5.70^{b}	14.20±5.16^{ab}	3.17±0.14^{b}	0.58±0.08^{b}	158.90±20.29^{b}
Blue	8.40±0.51^{c}	365.9±44.0^{b}	79.18±5.65^{b}	27.80±3.76^{a}	19.10±6.26^{b}	2.41±0.76^{a}	0.51±0.08^{ab}	145.70±8.33^{ab}
Red	9.30±0.48^{d}	229.9±50.3^{a}	80.51±6.93^{b}	27.40±6.80^{a}	22.00±3.05^{a}	2.68±0.23^{a}	0.45±0.04^{a}	134.10±10.10^{a}
F-values	129.59**	532.38***	21.70***	52.91***	8.13***	8.51***	28.46***	12.99***

Values are Mean ± SD; ***Indicate F-values to be significant at $P < 0.001$; For (a) Photo-periods: d.f. = 2, 27; Tukey's critical value = 3.51; For (b) Wave-lengths: d.f. = 3, 36; Tukey's critical value = 3.81; Mean values followed by the same letter are not statistically significant.

S. graminum population. Based on the assumptions given by Danks (1987), the photoperiodic responses classify any insect into one of the following category: (a) short photoperiod/ daylength induces development, (b) short photoperiod/ daylength accelerates development, and (c) intermediate photoperiod/ day length (close to the critical day length) accelerates development. Most of the insect species fall into the second category, *i.e.* accelerated development under short days in comparison to long days (Lopatina *et al.*, 2007).

Except at equator, each altitude shows a regular seasonal pattern of changes in day length and photoperiod is a stable indication of seasonal changes that induces the insect to prepare physiologically and behaviourally for such changes. It is often used by insects as a measure of seasonal change and as cues for activities including growth and development (Hodek *et al.,* 2012). Photoperiod guides insects to differentiate among the environmental fluctuations and to synchronize their timing of activities accordingly (Saikkonen *et al.*, 2012). The immature stages of the insects are also capable of perceiving changes in photoperiod and the extent to which these stages overlap with the shift in the critical photoperiod (Ruberson*et al.*, 2000). Thus, photoperiodic influence differs from species to species and even individuals of the same species (Fig. 8).

Danks (1991) observed that long photoperiod was accelerating growth in young larvae but decelerating the growth in older ones. When reared under two different photoperiods, *viz.* 14L: 10D and 24L: 0D, immaturestages of ladybird, *P. dissecta* had faster development with higher survival rates under 14L: 10D photoperiod (Mishra & Omkar, 2005). However, in ladybirds, *Coelophora saucia* (Mulsant) (Omkar & Pathak, 2006) and *H. axyridis* (Berkvens *et al.*, 2008) egg hatching rate was not consistently different under long and short photoperiods. But Omkar & Pathak (2006) reported maximum mortality in *C. saucia* under short day conditions followed by continuous day and long day conditions. Omkar & Singh (2007) found high incidence of pupation during late photophase and early scotophase in *M. sexmaculatus.* Under short day conditions, the pre-imaginal development was faster than under long day conditions in *H. axyridis* (Reznik & Vaghina, 2011). However, Omkar & Kumar (2016) found high prey consumption rates at long day lengths than at short day lengths. Such a behaviour in ladybirds further reveals that long photoperiodic conditions facilitates foraging and higher prey exploitation while short day lengths result in less prey consumption, conversion and utilization by the larvae (Singh *et al*., 2016a). Also, the higher mobility of prey during long days promotes their higher consumption by the ladybird predators (Kumar & Omkar, 2015; Omkar & Kumar, 2016).

Light intensity also significantly affects the ladybird bio-attributes. Since ladybirds are primarily diurnal insects and depend on visual cues and presence/absence of light to undergo various essential activities, like predation, mating, moulting and pupation (Mishra & Omkar, 2005; Omkar & Pathak, 2006; Omkar *et al*., 2006; Nalepa, 2013; Singh *et al*., 2016a). Shorter day lengths with the intensity of 1500 lux are beneficial for reproductive activities as it may shorten the pursuit times followed by increase in the duration of copula (Wang *et al.*, 2014). The white light is more suitable for essential activities compared to its red or blue components of the visible spectrum and these may influence the mating activity and predation performance of ladybirds (Omkar & Pathak, 2006; Table 5). Thus, light influences many aspects of an insect's life. Investigations of the complete photoperiodic and/or light intensity responses of insect pests and their predators are necessary to predict their phenology and potential geographic distribution (Koch & Galvan, 2008).

8. Genetic factors

It has been reported that the local populations of polyphagous insects that display variations in the use of host species are subject to natural selection for improved ability to use their own host (Via, 1990; Ueno *et al.*, 2001). Similar situations may also be applicable for the generalist predators, like the ladybird beetles. Since natural selection changes the frequency of alleles that control host use, genetic variation in growth performance on host species may change with each generation of selection (Ueno *et al.*, 2001). Therefore, within-population variations in the ability to use different hosts may reflect past selective forces. While assessing the genetic variation in growth performance in a population of the herbivorous ladybird beetle, *Epilachna vigintioctomaculata* Motschulsky on both the normal host and a novel host, Ueno *et al.* (2001) found higher heritabilities for growth performance on the novel host than the normal host. The results further pointed out that natural selection, which improved the ability of the population to use a particular host plant, had reduced genetic variation within that population in the ability to use that host plant.

Thus, estimation of the magnitude of genetic variation both within and among populations of polyphagous insects/ generalist predators is essential to understand the dynamics of host/prey species adaptation (Via, 1990). To understand this process of host/ prey species adaptation, however, requires elucidation of the presence and nature of genetic variation and covariation in differing the host/prey use within these populations of polyphagous insects/ generalist predators. Since selection changes gene frequencies; hence genetic variation may change at each generation of selection. Moreover, natural selection is thought to reduce genetic variation through the fixation and elimination of alleles in the population. But continual selection leads to an evolutionary plateau, as has been confirmed in experiments with small artificial populations (Hill, 1982). However, the effects of selection on genetic variation for natural populations, where the effective population size is often quite large, have yet to be established (Stearns,1992). Because, in a large population, it takes a long time for selection to eliminate genetic variation, and mutation will regenerate a certain amount of variation for polygenic characters.

Foraging behaviour of Coccinellidae

Hassell & Southwood (1978) have classified the environmental levels apparent to foragers in terms of prey, patch and habitats. This provides a framework for discussing the foraging behaviour of ladybirds. The adults locate patches of prey and their larvae feed on the prey in these patches. Movement between prey and within the aggregates of prey is referred to as local or *intensive search* (Bond, 1980) or area restricted search (Curio, 1976), between aggregates within patches is ranging or *extensive search*, between patches is *dispersal* and from patches to hibernation sites is *migration* (Ferran & Dixon, 1993; Hodek & Evans, 2012)(Fig. 9).

1. Pattern of foraging

Predators locate prey by extensive search and switch to intensive search once the feeding of prey initiates (Jander, 1975). If no further prey are captured, the predator gradually changes from the intensive to extensive search mode. The length of time spent in intensive search is called "*giving up time*". Extensive search is characterised by a relatively linear and fast movement, whereas local or intensive search is marked by sinuous, slow tracks interrupted by numerous stops. During a stop, larvae of Coccinellidae cast their body upwards and sidewards, thereby increasing the area within which prey may be located (Banks, 1957; Chandler, 1969). Intensive search is considered to be adaptive when predators hunt clumped prey, as it increases the chances of finding the prey (Dixon, 1959; Ferran & Dixon, 1993).

2. Orientation and prey recognition

During extensive and intensive search, ladybirds receive environmental and internal information (Papaj & Prokopy, 1989). These informations are used to orientate the ladybirds toward the prey; and are classified into two main groups (see Ferran and Dixon, 1993):

1. External sensory information: is typically visual, chemical or tactile. This information may be directional (visual stimuli, a trail, veins and edge of leaves) or non-directional (pheromone), and

2. Internally derived or internally stored information: are transmitted from proprioreceptors in or near locomotory organs and stored as individuals move, or acquired through learning or heredity.

3. Extensive search

Numerous studies have concluded that ladybirds do not perceive their prey before making any contact (Banks, 1957; Kaddou, 1960; Kehat, 1968); and consider that the efficiency of this random search is enhanced by both the predator and the prey, being negatively geotactic and positively phototactic.

3.1. Visual cues : Studies have suggested that adult ladybirds orientate visually to prey (Nakamuta, 1984, 1985). Moreover, both adults and larvae perceive colour contrast and orientate towards objects with the sharpest colour contrast relative to the background and prefer those objects with a complex shape (Said *et al.*, 1985; Harmon *et al.*, 1998; Wang *et al.*, 2015). Nakamuta (1985) have suggested that ladybirds are able to discriminate prey from non-prey like objects visually by their size and shape. Obata (1986) suggests that *H. axyridis* is capable of utilizing visual cues, such as green leaves, in locating prey. However, there are no evidences so far that can indicate that larvae use visual cues when foraging for prey.

3.2. Olfactory cues : Prey species secrete alarm pheromones in response to attack by predators, which causes other prey to disperse (Nault *et al.*, 1973). Synthetic (E)-farnesene, a principal component of aphid alarm pheromone, however, is supposed to behave as an olfactory cue for ladybirds (Nakamuta, 1991; Francis *et al.*, 2004; Hatano *et al.*, 2008; Singh *et al.*, 2016b). Aphid alarm pheromones have been found to attract*A. bipunctata* (Francis *et al.*, 2004), *C. septempunctata* (Al Abassi *et al.*, 2000; Ninkovic *et al.*, 2001), *C. maculata* (Zhu *et al.*, 1999), *H. axyridis* (Verheggen *et al.*, 2007), *H. convergens* (Acar *et al.*, 2001) and *M. sexmaculatus* (Singh *et al.*, 2016b). Obata (1986) and Meidari and Copland (1992), have also shown that ladybird species, *H. axyridis* and *Cryptolaemus montrouzieri* use olfactory cues to detect prey.

Das & Dixon (2011) have shown that honeydew contamination may be an important cue used by ladybirds when locating and assessing the abundance of prey in aphid colonies. In addition, aphid odour greatly influences oviposition and site selection in ladybirds (Evans & Dixon, 1986). This odour indicates the quantity and quality of their prey and mediates their oviposition responses (Sarmento *et al.*, 2007). Since prey quantity is a major limiting factor in attaining maximum ladybird oviposition, hence minimum density of aphids is required for oviposition (Mills, 1979; Dixon, 1959, 2000). The ovipositing ladybirds assess the patch quality of aphids for suitability of prey (Fréchette *et al.*, 2006), age of the aphid colony (Hemptinne *et al.*, 2000) and prey density (Oliver *et al.*, 2006) prior to oviposition.

Wang *et al.* (2015) studied the relative role of olfactory cues using foraging and foraging-experienced *P. japonica* adults and cotton plants with or without infestation by the cotton aphid, *A. gossypii*. Their results revealed that experienced beetles were more responsive to olfactory cues compared with beetles. The results, therefore, suggested that foraging experience might increase prey location in ladybird predators. However, Singh *et al.* (2016b) found that the ladybird, *M. sexmaculatus*, is able to perceive the presence of prey in its environment and modify its oviposition accordingly. Moreover, it is the perception of prey that influences oviposition more than the actual prey consumed. Further, the host plants may also provide olfactory and visual stimuli recognised by predators in the field, which may be missing in laboratory experiments and thus affect the choice of particular prey (Ninkovic *etal.*, 2001; Zhu & Park, 2005; Rondoni *et al.*, 2017).

3.3. Gustatory cues : Larvae of *C. septempunctata* may mark a plant chemically while searching for their prey (Marks, 1977; Kumar *et al.*, 2014c). This enables subsequent short-term recognition and avoidance of areas that have previously been searched. The semiochemical tracks left by larvae during foraging also serve several other functions, such as: (i) a means of avoiding cannibalism and competition with other aphidophagous ladybirds (Magro *et al.*, 2010), (ii) reduce overexploitation of a food resource limited in time and space (Nufio and Papaj, 2001), and (iii) signals for other species to prevent intraguild competition (Meisner *et al.*, 2011).

However, such markings do not affect the searching activity of other larvae. While making such markings, the ladybird larvae frequently touch the surface on which they are moving with their anal disk and their maxillary palps. The upper surfaces of the last segments of these appendages are covered with a thin membrane bearing gustatory sensilla. A chemical marker, therefore, could be produced in the anal region of the abdomen and could be perceived through sensilla on the maxillary palps (Barbier *et al.*, 1989).

4. Intensive search

The adoption of intensive search mode by ladybirds after ingesting prey (Nakamuta, 1984) but not after encountering aphid dummies indicates that the switch from extensive to intensive search results from ingestion of prey. For this reason, intensive search has also been called "*success motivated search*" by Vinson (1977). Chemical components of prey species, which stimulate changes in movements of ladybirds, are not known. As most ladybirds feed on a large number of aphid species, substances common to many aphid species might play this role (Hodek, 1973). Blackman (1967) has reported that *A. bipunctata* could not distinguish between the toxic aphid, *Megoura viciae* and the non-toxic aphid, *A. pisum.* In contrast, Dixon (1958) noted that as soon as *Adalia decem punctata* L.

penetrates the bodywall of the aphid, *H. pruni*, the prey was rejected. Thereafter, palpal contact is enough to reject this prey.

Thus, the chemicals excreted by aphids can induce intensive search. Carter & Dixon (1984) have further shown that the presence of aphid honeydew increased the time *C. septempunctata* spent searching for prey on plants. Thus, the important internal factor affecting intensive search of the predator, however, appears to be hunger (Carter & Dixon, 1982). The starvation causes ladybirds to adopt an intensive search mode before feeding and to search more intensively with less prey specific after feeding. The search becomes more and more intensive as shown by an increase in the number of stops, turn rate and a decrease in the rate of locomotion with starvation. But, without food for a too long period leads to a gradual decrease in activity, and finally the death of ladybird predator (Nakamuta, 1987) (Fig. 10).

5. Learning

If a species profits from experience, it can improve its foraging efficiency by responding appropriately to a changing environment (Drost *et al*., 1988). *Conditioning* is the most common type of learning and has been observed in order Coleoptera (Papaj & Prokopy, 1989). Conditioning may bring about changes in feeding preferences or affects the ways a ladybird forages. Every species of ladybirds prefers a particular habitat (Iperti, 1966), e.g., *C. septempunctata* is found mainly on herbaceous plants and *A. bipunctata* on trees. In their specific habitat, these ladybirds eat all the species of aphids they encounter. Thus, the foraging behaviour of the larvae varies according to the food they had previously eaten (Ettifouri & Ferran, 1993). Studies have shown that after feeding on the same food, the larvae changed from an extensive to an intensive search mode (Hattingh & Samways, 1995). But when they were fed a different food, the larvae either continued extensive search mode or adopted a less sinuous path than in the typical intensive search mode. These changes, although temporary, could further alter the predatory efficiency (Ferran and Dixon, 1993).

6. Factors affecting foraging behaviour

Foraging behaviour is affected by both the abiotic and biotic factors of the environment, and also by the physiological state of the predator.

6.1. Abiotic factors : Environmental conditions (temperature, humidity, light intensity) affect the searching behaviour of ladybird predators by modifying their rate of movement. Ladybirds warm up by absorbing solar radiations (Jankowsky, 1973). Rapid locomotion at high temperatures may be adaptive because predators need to find more prey to offset the depletion of their energy and water reserves. Desiccation often stimulates searching for prey because aphid prey is an important source of water. Moreover, climate may affect the distribution of predators on plants through its effect on the phototropic and geotropic responses. Curio (1976) suggested that the daily pattern in the search for prey is more or less dependent on the opportunities to feed rather than rigidly linked to circadian activity. Thus, the foraging behaviour of ladybird predators follows a rhythmical pattern controlled by a combination of endogenous factors and exogenous climatic components (Omkar & Pathak, 2006).

6.2. Biotic factors :

6.2.1. Plant : The orientation towards prey and the predatory efficiency of ladybirds, which have limited sensory abilities, depend on the physical and maybe chemical characteristics of plants (Carter *et al*., 1984; Jalali & Ziaaddini, 2017). Plant density, through its effect on the microclimate, affects both the ladybird abundance and the species composition. In cereal crops, the thermophilic ladybird, *C. septempunctata*, is the most abundant in low density strands, and *P. quatuordecimpunctata* prevails in dense strands (Honek, 1983).

The rate, at which a predator encounters a prey species, can be affected by the presence of hairs, pubescence, density of trichomes or waxes on the plant (e.g. Carter *et al*., 1984; Kumar *et al*., 1999; Timms *et al*., 2008; Karami & Shishehbor, 2012). Banks (1957) found that the larvae of the ladybird, *P. quatuordecim punctata*, moved more slowly on the hairy leaves of potato than on the glabrous leaves of bean. Moreover, the ladybirds, like many other predators, concentrate their search along the veins of leaves where aphid density is generally highest (Dixon, 1959). On leaves lacking prominent veins, ladybirds search the edge of leaves and the petiole (Carter *et al*., 1984). Reports are there that reveal that the last larval instars of *C. septempunctata* walk along the edges of wheat leaves clutching them with their legs and their anal pseudopod (Ferran & Deconchat, 1992), and then the prey searching adopt one of the four positions; sagittal, parallel, angular or overlapping. Whatever position the larvae adopt, the central area of the leaf is not searched as aphids are not found there.

The physiological state of a plant may also affect the foraging behaviour of a ladybird predator. Kesten (1969) has reported that adult *Anatis ocelata* L. test pine needles with their mandibles and only search new needles, presumably to reduce the amount of time in searching areas where the prey are not likely to be present. Plant structure may protect the aphids from predators. For example, third and fourth instar larvae are unable to enter the space between the stem and the ear of wheat, where the aphid *R. padi* is often to be found.

6.2.2. Prey : In ladybirds, resource quality affects the duration and speed of search, capture rate, the run/ stop ratio and the change from intensive to extensive search, which keep the predators longer in prey rich patches than in poor patches. Most research on prey quality is concerned with the nutritional value of various prey species (Omkar & Bind, 2004; Omkar & Mishra, 2005; Omkar, 2006; Kumar *et al*., 2013; Patel *et al*., 2017). As the adoption of an intensive search mode follows the ingestion of suitable prey (Nakamuta, 1984) the locomotory patterns of predators may be linked to prey quality. This is confirmed by the results of Houck (1986) and Ettifouri & Ferran (1993). The response to prey quality possibly depends on the food specificity of predators (Pervez & Omkar, 2004a; Omkar *et al*., 2009a, 2011). The duration of intensive search is also related to the size of the prey consumed. *Coccinella septempunctata brucki* showed significantly longer periods of intensive search when fed first a small then a large aphid than *vice versa* (Nakamuta, 1985).

The consumption of prey per unit time usually increases along with prey density until the predator is satiated. This is known as functional response (Holling, 1959) and can take one of the four forms, as describe above. Thus, the forager may:

1. Learn to find prey more readily at some critical prey encounter rate and then concentrate feeding on it
2. Spend less time in non-foraging activities at high prey encounter rates
3. Emigrate from prey patches more readily at low prey densities

Distance between patches and the distribution of prey within patches may also affect the foraging behaviour and searching success of predators. Murakami & Tsubaki (1984) conducted experiments on the searching efficiency of *C. septempunctata brucki* when attacking prey populations with different distributions and densities. They showed that searching efficiency depended on the prey distribution. At low prey density, the predator is most efficient when the prey is distributed uniformly whereas at high prey density, it is most efficient when prey is highly aggregated.

The response of prey to the presence of ladybirds can have an important effect on their foraging success (Dixon, 1958). Many aphid species respond visually to walking ladybirds (Klingauf, 1967), to tactile stimuli, plant vibrations induced by predators (Brodsky & Barlow, 1986) and olfactory stimuli, such as the alarm pheromone secreted by captured aphids (Ferran & Deconchat, 1992). Further, the most active forms of avoidance shown by the aphid prey are walking away, kicking and dropping. Dropping from plants is a fairly common response but is not without risks (Dixon, 1958) as aphids frequently fail to find another plant (Roitberg *et al*., 1979) and may be captured by ladybirds walking on the ground, as reported earlier by Ferran *et al*. (1991). Physical structures, such as the thickness of the cuticle, length of appendages and overall body size, may affect the acceptance of particular prey by ladybirds (Nedved & Salvucci,2008). An easy way of avoiding being eaten is to be toxic, unpalatable and defended chemically; and the siphuncular wax is the mostobvious chemical defence of many aphids against predators, including the ladybird larvae (Pasteels, 2007).

6.2.3. Predators : All species show changes in their pattern of movement following feeding and the area they traverse per unit time depends on their size or age. The first instars, which only search a very small area, are poor at capturing prey, and this stage is a critical period in a ladybird's development (Dixon, 1958, 1959). Newly hatched larvae remain on the egg cluster for some time after hatching and feed on unhatched eggs. It is generally believed that such sibling cannibalism benefits the survival of the remaining individuals, enabling them to make a more prolonged search for the prey (Dixon, 1959). Further, the crowding of conspecific larvae, to a certain optimum level, promotes social feeding and affects their development, survival and adult size, resulting in shortening of developmental duration, increasing immature survival and percent adult emergence than singly reared larvae (Omkar & Pathak, 2009). However, above the optimum level, crowding promotes intraspecific competition among the larvae, negatively affecting their growth and development (Omkar & Afaq, 2009; Bista *et al*., 2012; Table 3, 4).

Moreover, while exploiting the aphid colonies, both larvae and adults of ladybirds leave their footprints (*i.e*., semiochemicals) as they walk (Kumar *et al*., 2014c). These secretions contain non-volatile hydrocarbons~~,~~ and act as signals for predators to identify previously searched areas and cues for prey species in detection of predators (Magro *et al*., 2007; Ferrero *et al*., 2011). Chemical analyses show that tracks of different species vary greatly (Hemptinne *et al*., 2001; Michaud & Jyoti, 2007). The female ladybirds refrain from laying eggs, and the larvae desist from exploiting the aphid colonies, where they perceive the presence of semiochemical tracks left by other ladybirds (see Kumar *et al*., 2014c).

6.2.4. Intraspecific competition : Ladybirds generally aggregate on plants where prey is abundant (Huffaker *et al*., 1971). However, the intensive search mode and inactivity of ladybirds when satiated result in their aggregation in areas of prey abundance (Dixon, 1959; Kareiva & Odell, 1987). Following the rise in the density of ladybirds, the total number of prey consumed increases at a decreasing rate, while the rate of consumption per individual, which is at maximum when few predators are present, decreases (Bista *et al*., 2012). This results from rapid prey depletion and mutual interference between ladybirds, which induces them to scatter (Eveleigh & Chant, 1982). Such mutual interferences cause the ladybirds to fall off a plant, switch from intensive to extensive search and ultimately the ladybirds stop feeding (Ferran & Dixon, 1993).

CONCLUSION

Analysis of food relationships in ladybirds may be helpful in forecasting their activities in agricultural fields and improving their impact in relation to conservative and augmentative biological control strategies for insect pests. While the prey of ladybirds is classified as essential, alternative, rejected and toxic, the ladybirds prefer essential prey to perform best in terms of egg maturation, oviposition and development. Till date, numerous factors have been found to affect the prey preference in ladybirds, *viz*., prey species, prey abundance, mobility and defence of prey, morphological character and previous feeding experience of predator, predator and prey size, environmental and genetic factors. However, there are evidences that numerous cues guide the feeding behaviour of ladybirds. Amongst them are the volatiles of plants and/or of prey, aphid alarm pheromones and oviposition-deterrent chemicals in larval tracks.

Since the food resources of phytophagous and coccidophagous ladybirds are rather stable, specialized adaptive characteristics have evolved in aphidophagous species under the pressure exerted by the inherently ephemeral occurrence of their prey. This constraint has led to the evolution of a number of adaptive life-history traits, such as, fast development, high adult mobility, high speed of larval movement and reversible oosorption (see Hodek *et al*., 2012). Future studies in ladybirds may be designed targeting such evolutionary aspects. Further, the study of ladybird orientation to volatiles has not progressed beyond laboratory tests, and field assays are still needed to validate the laboratory findings. In searching for an oviposition site, there is a trade-off for ladybirds between two factors: whether to lay eggs near to prey so that first instars find their prey early, or to reduce attacks by conspecific or heterospecific ladybirds on offspring by ovipositing farther away. Such hypotheses need to be further tested, both in laboratories and under field conditions.

Moreover, the adequacy of prey is generally established after assessing the life-history parameters of ladybirds, such as their successful completion of larval development and high reproductive performance. While earlier researches have worked with single prey, some recent studies have revealed the importance of mixed food. However, modern serological and molecular methods have been developed so far to detect the type of prey consumed by predators (Rondoni *et al*., 2015). Still the classical microscopical analysis of food remnants from the gut can also yield precise evidences (see Hodek *et al*., 2012). Future studies on prey-predator relationships in Coccinellidae may be designed exploiting such methods.

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