2. REVIEW OF LITERATURE

In view of increasing awareness of sustainable agriculture in recent times, much attention is being paid to utilize biocontrol agents in the control of insect pests instead of spraying large amount of pesticides (Kajita et al., 2000). Biological control is the most economical, ecofriendly and effective approach involving the utilization of natural enemies such as predators, parasitoids and pathogens. The predaceous coccinellids under the order Coleoptera and family Coccinellidae are linked to biological control more than any other taxa of predatory organisms. The beneficial status of these organisms has a rich history which has been recognized by many biological control practitioners (Hodek, 1973; Hodek and Honek, 1996; Klausnitzer and Klausnitzer, 1997; Honek et al., 2013).

Individuals of the family Coccinellidae are important predators of aphids (Hodek, 1973; Hagen, 1974; Frazer, 1988), mealybugs (Hagen, 1974; Herren and Neuenschwander, 1991), mites (Hagen, 1974; Chazeav, 1985), scale insects (DeBach and Rosen, 1991), whiteflies (Gerling, 1990), etc. Of the 6000 species of coccinellids world-wide (Vanderberg, 2002) more than three hundred species of predaceous coccinellids have been reported from India (Poorani, 2004; Satpathi, 2009). The first major success
of biological control was achieved with the introduction of Australian ladybird beetle, *Rodolia cardinalis* in California for the suppression of *Icerya purchasi* and threat to the citrus production posed by this scale insect was successfully averted (Doutt, 1964). This success led to the advent of ladybird fantasy period, a period involving widespread and haphazard introduction of predaceous ladybirds throughout the world (Lounsbury, 1940). It led to an intensive research on ecological aspects of predaceous ladybeetles including their interaction with prey and other heterospecific predators. The book on ladybirds by Hodek and Honek (1996), Majerus (1994), Klausnitzer and Klausnitzer (1997) and Dixon (2000) gave excellent general accounts and coverage of extensive literature. The published works on ecology have been supplemented with a small number of reviews (Hagen, 1962; Hodek, 1967; Strand and Obrycki, 1996; Obrycki and Kring, 1998). Hodek (1996) presented an exhaustive review on ecology of coccinellids including important aspects such as phylogeny variability, genetic studies, development and distribution beside their effectiveness and utilization as biocontrol agents. Prey-predator interaction of ladybeetles and their applications in biocontrol has been extensively studied (Dixon, 2000; Omkar and Pervez, 2002; Dixon and Agarwala, 2002; Agarwala *et al.*, 2003a). In addition, the importance of certain ladybirds as biocontrol agents has been discussed in recent reviews, eg. *Cheilomenes sexmaculata* (Fabricius) (Agarwala and Yasuda, 2000), *Coccinella septempunctata*
Linnaeus (Omkar and Pervez, 2002), *Chilocorus nigritus* (Omkar and Pervez, 2003) and *Harmonia axyridis* (Pallas) (Koch, 2003; Pervez and Omkar, 2006).

Melanaphis donacis (Passerini), Macrosiphum rosaeformis (Das), Macrosiphoniella sanborni (Gillette), Megoura cajani Ghosh, Ghosh and Raychaudhuri, Toxoptera citridicus (Kirkaldy), Rhopalosiphum maidis (Fitch), Cervaphis quercus Takahashi and Tuberculatus nervatus Chakrabarti and Raychaudhuri (Singh et al., 2013). Omkar and Pathak (2006) also reported *M. persicae* to be an essential food of *C. saucia*.

*C. saucia* (Plate 2) is characterized by the large sub-elliptical red or fulvous spot on the middle of its black elytra. The insect is holometabolous with egg, larva and adult included in its developmental stage. Preliminary studies on the biology of *C. saucia* were carried out by Tao and Chiu (1971), Hsieh et al. (1985), Dai (1990), Singh and Singh (2002), Omkar et al. (2006) which included its seasonal occurrence, feeding potential, functional response, developmental duration, consumption of eggs in presence of aphids. Omkar and Pathak (2006) studied the influence of photoperiod and wavelength on the pre-imaginal development and reproductive performance of *C. saucia*. Certain reproductive attributes have also been reported recently by Omkar et al. (2010b). However, a review of literature from the past few decades clearly elucidates those relating to bioecology, prey consumption and effect of prey density, conspecific and heterospecific predators on the life history of *C. saucia* in relation to *A. craccivora* to be vague and fragmentary.
Aphis craccivora Koch (Plate 1 and 4) is a serious polyphagous pest (Ghosh, 1975) of leguminous crop plants in South-East Asia and is highly prevalent throughout India (Tao and Chiu, 1971; Agarwala et al., 1987). Both nymphs and adults suck plant sap and cause serious damage right from the seedling to pod bearing stage. A. craccivora also injects toxin into the plant while feeding which reduces the vigour and yield of the plants (Radha, 2013). Dhingra (1994) reported development of resistance by this pest to various pesticides. A. craccivora has been reported to have a wide range of host plants from India (Poddar, 1982). Some of the host plants of this aphid include economically important pulses viz., groundnut, Arachis hypogea L. (Parsana et al., 1997), cowpea, Vigna unguiculata (Linn.) (Hijam and Singh, 1989; Munyuli, 2009), green gram, Phaseolus aureus L. (Das and Dutta, 1999), broad bean, Vicia faba (Zhou Hui et al., 1984), Chickpea, Cicer arietinum Linn. (Sithananthan et al., 1984), mung bean, Phaseolus mungo (Li-Dx et al., 1994), country bean, Dolichos lablab (Agarwala et al., 1987) and rice bean, Vigna umbellata (Singh and Singh, 2002). Their association with other aphidophagous predators on various leguminous crops has been reported by Singh (2002) and Singh et al., (2011).

Since the present work deals with bio-ecology and predator-prey relationship, an attempt has been made to review the available information
on the population dynamics, development and somatic growth rate, reproductive fitness and intraguild interactions of the coccinellid predator, *C. saucia* in relation to its aphid prey *A. craccivora*.

### 2.1. SEASONAL ABUNDANCE OF PREDATOR AND APHID PREY

Assessment of insect population is a pre-requisite for successful pest management programme and is related to the extent of damage caused by the pest. The population dynamics of a species necessitates knowledge of the numerical changes that occurs in the population and analysis of the factors causing them. Population of insects in nature fluctuates due to the effect of a number of density dependent and independent factors (Varley *et al.*, 1980) as well as the food quality of the host plant (Dixon, 1970).

Several authors have opined that aphidophagous insects play an important role in determining the abundance of aphids. The effectiveness of coccinellid predators in controlling aphid populations has been studied by Hodek (1967), Van Emden *et al.* (1969) and Van Emden (1988). However, the rate of increase of aphids is reported to be frequently restrained by intraspecific competition for resources (Dixon and Kindlmann, 1998). Sequeira and Dixon (1997) and Dixon and Kindlmann (1999) also attributed the fluctuation of aphid abundance from year to year to intraspecific competition between the aphids. Thus, in absence of long-term studies on the population dynamics of predatory ladybirds, their precise role
in determining aphid abundance will remain debatable. Heathcote (1978) meticulously observed the abundance of the cereal aphids and the number of hibernating ladybirds over a period of 15 years in order to resolve this issue. Carter et al. (1982) reported that swarms of ladybirds coincide with outbreaks of cereal aphids. Meanwhile Hodek et al. (1972) discussed the methodologies used to measure the impact of predators on prey population and remarked that most of the studies on predatory efficiency were based on correlation between predator’s abundance and changes in prey population. Several workers have also observed density-dependent relationship between the seasonal population of aphids and their natural enemies (coccinellids) in several agro-ecosystems in different parts of India (Venugopal et al., 1978; Shukla and Pathak, 1987; Debaraj and Singh, 1990; Jalali et al., 2000; Rana et al., 2001; Paul and Konar, 2005; Lokeshwari and Singh, 2008; Bilashini and Singh, 2010, 2011).

2.1.1. Coccinellids

A review of literature revealed that most of the work pertaining to population studies had been carried out on different coccinellid beetles other than *C. saucia*. Tao and Chiu (1971) after an extensive study on the biological control of citrus, vegetables and tobacco aphids along with their natural enemies concluded that *Lemnia swinhoei* Crotch (now *C. saucia*) was the most abundant aphidophagous coccinellid in Taiwan. The
population abundance of coccinellid species in relation to aphid infesting cotton was studied by Bishop and Blood (1978) and suggested that coccinellids could effectively maintain aphid population below crop economic injury levels in unsprayed cotton. Honek (1982) while analyzing the factors influencing the population density of the adult *Coccinella septempunctata* and *Coccinella quinquepunctata* observed significant relation between primary parameters of aphid and coccinellid density. Hseih *et al.* (1985) reported 12 species of predaceous ladybug including *L. swinhoei* that feeds on mulberry psyllid from Taiwan. Singh and Singh (1985) reported presence of various aphidophagous coccinellids including *C. saucia* and their period of activity in Manipur. Maximum aphid population in absence of predators and minimum under natural condition was suggested where predators played a positive role in regulating aphid density (Gupta and Yadav, 1989). Mani and Krishnamoorthy (1989) studied the impact of insect predators in the control of *A. gossypii* Glover on guava. They observed five coccinellid predators (*viz.*, *Menochilus sexmaculata* F., *Scymnus* sp., *Pseudospidimerus circumflexa* (Mots.), *Chilocorus nigritus* F. and *Cryptolaemus montouzieri* Muls.) and two syrphid predators feeding on *A. gossypii*. In Yangzhou area of China, Dai (1990) made a study on the seasonal occurrence of *C. saucia* and its predation rate on aphids. He concluded that *C. saucia* played an important role in suppressing the aphid population. Seasonal population fluctuation of cowpea aphid, *A.*
craccivora and its predatory coccinellids was observed by Srikanth and Lakkundi (1990) in Bangalore and concluded a strong significant correlation between aphid and predator populations in two observed seasons. Cheng et al. (1992) studied the seasonal occurrence of sugarcane woolly aphid and its predators on autumn planted canes and observed *Lemnia saucia* to be an important predator of *C. lanigera*. Shantibala et al. (1994) while assessing the abundance of aphid *Cervaphis rappardi indica* observed 7 species of predatory coccinellids including *L. saucia*. The population dynamics of bean aphid, *A. craccivora* Koch and its predatory coccinellid complex in relation to crop type and weather conditions were studied by Sharma and Yadav (1994) in Bihar. Veeravel and Baskaran (1995) showed the effectiveness of third instar grubs and adults of two coccinellids viz., *C. transversalis* and *M. sexmaculatus* in lowering the population of *A. gossypii* on brinjal plants through different predator-prey ratios. Devi et al. (1996) studied the impact of natural enemies including coccinellids on *M. persicae* infesting cabbage. Sarma et al. (1996) reported 4 coccinellid predators viz., *L. biplagiata, C. transversalis, Micrapis discolor* and *C. sexmaculata* from green gram infested with *A. craccivora* and concluded that the populations of *L. biplagiata, M. discolor* and *C. sexmaculata* was low and sporadic. Joshi et al. (1997) in the survey of host range and predatory fauna of *A. craccivora* in Bangalore recorded eleven coccinellids, six syrphids, a chaememyiid and a hemerobiid species.
Among the coccinellid predators, \textit{C. sexmaculata} was found to be predominant. Study of numerical response of \textit{C. sexmaculata} and \textit{C. transversalis} in the bean field suggested that adults of the beetle became active at low aphid density/plant and closely synchronized their aggregation and reproduction with natural population of \textit{A. craccivora} (Agarwala and Bardhanroy, 1997; Agarwala and Yasuda, 2000). Narang and Rana (1999) observed the population of the predator, \textit{C. septempunctata} to be prey density dependent. Wells and McPherson (1999) in population dynamics study of coccinellids in flue – cured tobacco plant infested with tobacco aphid, \textit{M. nicotianae} concluded that coccinellids collectively might be important biological control agents of tobacco aphids. Singh and Singh (2000) studied the role of biotic and abiotic factors on the population trend of \textit{A. glycines} on soybean in Manipur. The study revealed 5 coccinellids (\textit{C. transversalis, M. sexmaculatus, L. saucia, L. bisellata} and \textit{Scymnus} sp.) to associate with the aphid and exhibited positive relation with the aphid density. Afroze (2001) observed the relative abundance of aphids and their coccinellid predators and obtained significant positive correlation between the aphid species and their coccinellid predators. Singh and Singh (2002) studied the role of aphidophagous predators viz., \textit{L. saucia, M. sexmaculatus, Symnus} sp., \textit{I. scutellaris} and fungal pathogens in the suppression of \textit{A. craccivora} Koch on rice bean in Manipur. Five species of aphidophagous coccinellids viz., \textit{H. undecimnotata, Adalia bipuncta,}
Adonia variegata, Propylea quatuordecimpunctata and C. septempunctata were recorded as dominant predators while studying the seasonal abundance of M. persicae on tobacco (Nickolas et al., 2004). Singh and Singh (2005) studied the growth rate of aphids and their coccinellid predators on rape crop in Bareilly and observed a density dependent relationship between the two. Honek and Martincova (2005) assessed long term changes in abundance of C. septempunctata in Czech Republic. Seasonal incidence of predators associated with A. glycines in commercial soybean fields was studied by Mignault et al. (2006) in Quebec. Khan et al. (2007) studied the relative abundance of predaceous ladybird beetles in fruit, cruciferous crop, forest and floriculture and ornamental ecosystems of Kashmir and revealed a total of 15 predaceous species. Sarma et al. (2007) studied the population fluctuations of C. lanigera and its natural enemies in sugarcane crops in Assam and concluded that Coelophora biliagia along with other natural enemies had a significant positive impact on the aphid population. Mandal and Patnaik (2008) studied the interspecific abundance and seasonal incidence of aphids and aphidophagous predators associated with cabbage. A total of 4 species of coccinellid predators viz., C. transversalis, C. sexmaculata, M. discolor and C. septempunctata were found to be associated with the three prey aphid species. Singh et al. (2008) evaluated the effectiveness of three bio-agents viz., C. septempunctata, Chrysoperla carnea and Verticillium lecanii
(Zimm.) against mustard aphid and found *C. septempunctata* to be most effective by reducing aphid population to 88% after 10 days of release. The study on the effects of variety of native insect predators on population densities of *A. craccivora* indicated that release of predators at the ratio of 3:2:1 (ladybeetles: syrphid larvae: earwigs) per 1000 aphids in each cage significantly reduced the aphid population in the cowpea and groundnut fields (Munyuli, 2009). Seasonal dynamics of *A. gossypii* and relative abundance of its coccinellid predators on cucumber was studied by Lokeshwari *et al.* (2010b). Meanwhile population build-up of aphidophagous coccinellid, *C. septempunctata* in relation to aphids infesting cruciferous crops in Manipur was studied by Singh and Lokeshwari (2010) and Bilashini and Singh (2011). Sarma *et al.* (2011) observed the seasonal abundance of coccinellids predating upon cowpea aphid, *Aphis fabae* Scopoli at Solan and the study revealed occurrence of six coccinellid species. Singh *et al.* (2011) observed the diversity of predatory complex of *A. craccivora* on pulse crops in Manipur and recorded a total of 15 species including *C. saucia* to be associated with it. Ghosh and Chakraborty (2012) studied the incidence and abundance of important predatory beetles with special reference to *C. septempunctata* in Sub-Himalayan region of north-east India. Vandereycken *et al.* (2013) evaluated the abundance of adults, larvae and pupae of *H. axyridis* in four agronomical crops (wheat, corn, broad bean and potato) in Belgium.
**Aphids**

The populations of insects in nature are known to fluctuate due to the effect of various density dependent and independent factors. Aphids being small and soft-bodied insects are vulnerable to both biotic and abiotic interferences (Dixon, 1985) resulting in their population fluctuation. Aphids are known to exploit their ephemerally nutritious habitats by rapidly producing several progeny when conditions are favourable, but some also divert more of their resources into stored fat (Dixon and Wellings, 1982). Food quality and temperature that vary greatly during the course of a season have a marked effect on the development, reproduction and survival of aphids (Dixon *et al.*, 1982). Population studies of aphids in relation to their seasonal variation and abiotic factors have already been investigated for several economically important aphid species such as *Brevicoryne brassicae* (L.) (Hughes and Gilbert, 1968; Kotwal, 1982; Debaraj and Singh, 2004), *Acyrthosiphon pisum* (Harris) (Frazer and Gilbert, 1976; Soroka and Mackay, 1990), *A. gossypii* Glover (Paul and Konar, 2005; Das *et al.*, 2006), *Lipaphis erysimi* Kalt. (Singh and Singh, 1994; Devi *et al.*, 1997), *Macrosiphum rosaeformis* Das (Agarwala and Raychaudhuri, 1981; Kakkar and Sood, 1989), *Myzus persicae* Sulzer (Verma and Parihar, 1996; Bijaya *et al.*, 2006).
Studies on the population dynamics of *A. craccivora* had already been conducted by Davies (1972) and Guitierrez *et al.* (1974) on groundnut. Patel *et al.* (1976) studied the population of *A. craccivora* and observed a decrease in the aphid population with an increase in the population of natural enemies. The population incidence of *A. craccivora* and their coccinellid predators were observed on cowpea in Assam (Saharia, 1980). Hijam and Singh (1989) studied the seasonal incidence of *A. craccivora* infesting cowpea in Manipur at two different altitudinal regions and found that numerical abundance varied at the two study sites. Faleiro *et al.* (1990) recorded the influence of abiotic factors on the population build up of important insect pests of cowpea and their biotic agents. Malik *et al.* (1991) investigated the effect of biotic and abiotic factors on the multiplication of *A. craccivora*. Singh and Singh (1991, 1995) observed an unusual high incidence of bean aphid, *A. craccivora* on the soybean varieties and leguminous weed at Sehore in Madhya Pradesh. Barman and Dutta (1995) studied the seasonal incidence of *A. craccivora* on summer green gram in Assam. Parsana *et al.* (1997) studied the association of *A. craccivora* with coccinellid predators and their relation to abiotic factors. The aphid appeared in early July, reached peak population in early August and then diminished in late August. Joshi *et al.* (1997) conducted a survey on the population of *A. craccivora* during summer and kharif seasons. Slman and Mohamed (2000) studied the occurrence and abundance of *A.
craccivora infesting faba bean plants in Upper Egypt and found that the population of both apterous and alate forms of the aphids was highest in December of both seasons. Das and Dutta (2002) also recorded peak infestation of A. craccivora in 2nd week of December in green gram varieties.

Banerjee and Bandyopadhyay (2005) studied the population build up of A. craccivora in different cropping seasons on three crops viz., groundnut, rice bean and green gram. Hossain et al. (2006) studied the relative abundance of A. craccivora in relation to different sowing dates and recorded that aphid population and infestation increased with the delaying dates of sowing. Ahmad and Kumar (2007) observed the food plants and natural enemies of A. craccivora in Northeast Bihar. Their study revealed that the intensity of aphid infestation varied depending upon the food plants and localities. Rakshani et al. (2009) investigated the population dynamics of three alfalfa aphids viz., A. pisum, Theroioaphis trifolis forma maculata (Buckton) and A. craccivora and their most abundant predators and parasitoids in three sites of Iran and reported that frequency and temporal occurrence of alfalfa aphid in different regions varied and the population of aphids were mainly affected by alfalfa harvesting, ambient temperature and the coccinellid predators. Dubey and Singh (2011) studied the population dynamics of A. spiraecola on medicinal plants in eastern U.P. Kandakoor et
*al. (2012) recorded the incidence and abundance of sucking pests on groundnut. Recently Majumder and Agarwala (2013) studied the population dynamics of *Ceratovacuna silvestrii* and its coccinellid predator, *Anisolemnia dilatata* on bamboo plants in north-east India.

Understanding the effect of environmental factors on the occurrence and incidence of pest and natural enemies is important in developing control strategies. Becker (1974) opined that the size of population of pests and their extent of damage in a region may be governed by environmental factors and natural enemies. Climatic factors like temperature and humidity have been essentially reported to influence the biological responses of aphids as in *Toxoptera aurantii* on orange plants (Agarwala and Bhattacharya, 1995) and *A. fabae* on sugarbeet (Camprag *et al.*, 1990). Leather *et al.* (1989) reported that temperature had a marked effect on the reproductive rate of *R. padi*, wherein a higher reproductive rate was achieved at 20°C compared to 15°C. In general, several authors have reported the importance of environmental factors viz., temperature, relative humidity, rainfall, sunshine and windspeed in regulating the populations on several crop ecosystems (Debaraj *et al.*, 1994; Singh, 1997; Singh and Singh, 2000; Rana *et al.*, 2001; Dhaliwal and Singh, 2004; Banerjee and Bandyopadhyay, 2005; Das *et al.*, 2006; Bhatt *et al.*, 2007; Patel *et al.*, 2010; Majumder and Agarwala, 2013).
Faleiro et al. (1990) reported that an increase in sunshine hours and maximum daily temperature significantly increased aphid population in the field. However, these factors were of no significance with the performance of aphids in certain cases (Jalali et al., 2000; Dhallwal and Singh, 2004; Banerjee and Bandyopadhyay, 2005). Ferran and Larroque (1980) opined abiotic factors to be among the most important factors influencing the growth and development of ladybird beetles. Among all the density dependent factors, temperature has been reported to affect the different biological rates particularly of predators (Frazer, 1988). Phoofolo and Obrycki (2000) stated that abiotic factors also govern the ability of ladybeetles to successfully invade new habitats.

Hijam and Singh (1989) discussed the population fluctuation of both the pest, *A. craccivora* and its predators in relation to abiotic factors at two different altitudinal regions. Raj (1989) while studying the seasonal abundance of natural enemies of aphids infesting potato crop recorded the population build-up of *C. septempunctata* to be positively correlated with temperature and morning humidity whereas *M. sexmaculatus* population build-up was negatively correlated with temperature and afternoon humidity. The importance of abiotic factors mainly rainfall in lowering the predators population was suggested by Srikanth and Lakkundi (1990) while studying the correlation between *A. craccivora* and its predators. Studies on
the seasonal relationship between changing populations of *L. erysimi* and its predatory coccinellids in rapeseed mustard crop ecosystem revealed that both the pest and predator reacted sharply to the changing temperature and relative humidity but almost in opposite directions. Singh and Singh (1994) reported that abiotic (temperature, relative humidity, wind velocity, sunshine and rainfall) and biotic factors (predators) jointly contribute for 77.69% and 62.68% impact respectively on the population dynamics of *L. erysimi*. Shantibala *et al.* (1994) reported a weak negative correlation of *C. rappardi indica* with temperature and rainfall. Meanwhile it exhibited weak positive correlation with relative humidity and vice versa with coccinellid predators. Verma and Parihar (1996) studied the appearance, critical level and peak incidence of *M. persicae* on potato crop in relation to weather factors. Its appearance was significantly correlated with variations in temperature and upto critical level, humidity and rainfall played some role. Multiple regression equation for temperature and rainfall together showed the ability to explain 60.6% variation in the population growth. Parsana *et al.* (1997) studied the association of *A. craccivora* with coccinellid predators and their relation to abiotic factors. They observed that the aphid population was positively correlated with relative humidity and rainfall and negatively with maximum temperature whereas the population of coccinellids was not greatly influenced by the weather factors, but by the fluctuations in the aphid population. Narang and Rana (1999) recorded the
role of biotic and abiotic environment on seasonal incidence of corn leaf aphid, *R. maidis* (Fitch) on barley. Jalali *et al.* (2000) reported that among the abiotic factors, relative humidity and temperature significantly affected the population of *A. gossypii* and its natural enemies. Rana *et al.* (2001) recorded that low temperature and high humidity along with higher degree of rainfall and hailstone adversely affected the population of mustard aphid, *L. erysimi* in Uttaranchal. Parihar *et al.* (2001) reported that rainfall favoured the population build-up of coccinellid predators while atmospheric temperature and relative humidity played marginal role. Veeravel and Jaganathan (2002) studied the influence of weather parameters on the population dynamics of *A. gossypii* and its predator, *C. sexmaculata* in cotton ecosystem. Saminathan *et al.* (2003) studied the correlation between coccinellid, *M. sexmaculatus* and major weather factors on cotton. Maximum temperature and rainfall was negatively correlated with coccinellid population while minimum temperature, relative humidity and sunshine exhibited positive correlation. A study on population dynamics of *B. brassicae* in relation to abiotic and biotic factors revealed that decrease in temperature and rainfall favoured the population build-up of the pest and the numerical abundance of the predators coincided with that of the pest (Debaraj and Singh, 2004). Paul and Konar (2005) also studied the population dynamics of *A. gossypii* in relation to abiotic and biotic factors in West Bengal and concluded that abiotic factors have great influence on
the population dynamics of aphids than the biotic factors. Banerjee and Bandyopadhyay (2005) studied the influence of weather parameters on the population build-up of *A. craccivora* in different cropping seasons. Das *et al.* (2006) observed significant role of abiotic factors in population build-up of *A. gossypii* on cucumber. Tank and Korat (2007) and Lokeshwari and Singh (2008) established negative correlation of abiotic factors with the predator population. Shantibala *et al.* (2009) studied the impact of climatic changes on vulnerability of oak aphids and their natural enemies in Manipur. Correlation analysis between independent variables such as average temperature, relative humidity and total rainfall with predator population revealed both positive and negative association. They concluded that temperature is probably the single most important environmental factor influencing insect behavior, distribution, development, survival and reproduction. Bilashini and Singh (2010, 2011) studied the relative abundance of *L. erysimi* and *C. septempunctata* in relation to weather parameters on cruciferous crops. Temperature, relative humidity and rainfall showed negative correlation with prey and predator population whereas sunshine and windspeed showed positive correlation. Ghosh and Chakraborty (2012) recorded the incidence of *C. septempunctata* to be positively correlated with temperature and vice versa with relative humidity. Javed *et al.* (2013) studied the population dynamics of insect
pests of safflower and observed positive correlation of aphid population with temperature.

2.2. EFFECT OF PREY DENSITIES ON LARVAL DEVELOPMENT

2.2.1. Functional response of coccinellids

Functional response is the study of the impact of insect predators on varying prey density (Solomon, 1949; Holling, 1959). It is a key factor regulating the population dynamics of predator-prey systems (Mandour et al., 2006). Functional response describes the rate at which a predator kills its prey at different prey densities and helps to estimate the efficiency of a predator in regulating prey populations (Murdoch and Oaten, 1975). Holling (1965) proposed four basic types of functional response by plotting the number of prey killed against the number of prey available and analyzing a continuum of patterns. Type – I response is the simplest in which the attack rate of individual increases linearly with prey density but suddenly reaches a constant value when consumer is satiated. In Type II (cystoid) response prey consumption increases curvilinearly with prey density reaching a plateau of satiation at higher prey densities and is common in most ladybirds (Hodek et al., 1984; Omkar and James, 2001; Xia et al., 2003). In type III response (sigmoid) attack rate accelerates initially and decelerates towards satiation. The responses of type I and II are
found in most invertebrates, whereas type III is more common in vertebrates, although some arthropods can also show this response when their preferential prey is not available (Hassell et al., 1977; Jervis and Kid, 1996). Few ladybirds especially acarophagous ones exhibit type III response. A type IV response (dome-shaped) occurs only when other prey of the same or of different species interfere in predator handling or if the prey show some kind of defensive behavior, which can intensify at higher densities.

According to Holling (1965) and Hassel et al. (1976) the functional response of a predator has components such as exposure time, prey searching time, instant discovery rate or attack rate and prey handling time which includes the time spent on attacking, killing, subduing and digesting the prey. Thus the study of different types of functional response is important in understanding the underlying mechanisms in predator-prey interaction, in elucidating the practical role of co-evolutionary relationships and in contributing towards biological control using this kind of interaction (Houck and Strauss, 1985). Hodek and Honek (1996) had reported the existence of all three types of functional responses viz., type I, type II and type III for coccinellids. The coccinellid, *H. axyridis* has been observed to respond differentially to different prey species i.e., type I on the aphid, *R. prunifoliae* (Lou, 1987), type II on the aphid, *L. erysimi* (He et al., 1994)
and type III on the aphid, *Cinara sp.* (Hu et al., 1989). Koch et al. (2003) reported a predator’s response to single prey type to differ within and between species. The increase in the number of prey killed with increased density is probably owing to the wider spacing out of prey at lower densities leading to increased time and energy expenditure of the predator in search of prey (Holling, 1966). The presence of asymptote at higher densities is likely to be function of satiation.

Sinha et al. (1982) studied the functional response of *C. septempunctata* at different prey densities of *L. erysimi* and revealed type II model. Ofuya and Akingbohungbe (1988) evaluated the density responsiveness of IV instar larvae of *C. lunata* in terms of functional response on *A. craccivora* under laboratory conditions and found that the number of prey consumed by each predatory stage increased more steeply than at higher prey densities. Predation rate of *C. saucia* under different prey densities was found to follow Holling type II equation (Dai, 1990). Babu and Ananthakrishnan (1993) studied the functional response of *C. transversalis* and *C. sexmaculata* on *A. fabae* and found that predatory efficiency and attack rate of predator were directly proportional to the prey density. Functional response study of adults and different larval instars of *Coelophora inequalis* on *A. craccivora* revealed that prey consumption rate increased upto a point with increasing prey density (Mora et al., 1995).
Wagiman (1996) conducted studies to determine the functional response of larvae and adults of *C. sexmaculata* on *A. gossypii* and found both the larvae and adult to exhibit Holling’s type II response. Agarwala and Bardhanroy (1997) observed the functional response of *C. sexmaculata* on *A. craccivora* and reported that prey consumption increased to a certain point with increase in prey density after which it became constant. Veeravel and Baskaran (1997) analyzed the functional responses of two ladybeetles, *C. transversalis* and *C. sexmaculata* on aphid, *A. fabae* and obtained Holling type II response in both cases.

Functional response of IV instar and adults of *H. convergens* exhibited type II response to density of aphid, *M. nicotianae* of which fourth instar had a higher search rate and longer handling time (Wells and McPherson, 1999). Functional responses of three voracious stages viz., fourth instar, adult male and female ladybeetles of *C. septempunctata* (Omkar and Srivastava, 2003a; Bilashini et al., 2010), *C. transversalis* (Omkar and James, 2001; Sarker et al., 2008) and *A. cardoni* (Omkar and Kumar, 2013) exhibited Holling type II response. Functional response was also studied in other ladybeetles viz., *P. japonica* (Kawauchi, 1979), *C. sulfurea* (Olivier) (Hodek et al., 1984), *C. vicina* (Mulsant) (Ofuya, 1986), *H. axyridis* (He et al., 1994), *H. conformis* (Boisduval) (Asante, 1995), *Propylea dissecta* (Omkar and Pervez, 2004), *Scymnus levallanti* and
Cycloneda sanguinea (Isikber, 2005), C. septempunctata and Chilocorus infernalis (Khan and Zaki, 2007), Eriopis connexa (Sarmento et al., 2007), Adalia tetraspilota (Hope), Calvia punctata (Mulsant) and Hippodamia variegata (Goeze) (Khan and Mir, 2008; Dehkordi et al., 2012).

2.2.2. Larval developmental duration

The prey quality and quantity has a major influence on the growth and development of predaceous insects, especially ladybird beetles. Agarwala and Yasuda (2000) opined that an estimate of larval development is considered reliable when the larvae are fed on optimal diet of most suitable aphids at constant condition. The predaceous coccinellids have a pronounced ability to adjust to food scarcity as an adaptation to an intermittent absence of prey. Larval development can also be completed on a fraction of the optimum amount of prey but the development is delayed and resulting pupae and adults have lower weight and are smaller in size. In addition, survivals of both larvae and adults have also been found to be decreased (Hodek, 1996).

Tao and Chiu (1971) reported that larvae of L. swinhoei can complete their life-cycle at 15°C though the optimum temperature for development is 25-28°C. Kawauchi (1979) evaluated the effect of temperatures on development of M. sexmaculatus and observed that as
temperature increased, developmental period tend to get reduced. Semyanov and Berezna (1988) studied the effect of temperature on the duration of development of *L. biplagiata*. The larval duration was observed to be 16, 10 and 8 days at the temperature of 20\(^\circ\)C, 25\(^\circ\)C and 30\(^\circ\)C respectively. Similar temperature dependent immature survival and development has also been reported in other ladybeetles (Obrycki and Tauber, 1982; Ponsonby and Copland, 1996; Bind, 1998; Srivastava and Omkar, 2003). Debaraj and Singh (1990) observed the mean duration of I, II, III and IV instar larvae of *C. transversalis* larvae to be 4.69, 3.62, 5.0 and 7.69 days respectively with a total larval period ranging from 19 to 23 days when fed on *A. craccivora*. Developmental rate of *C. saucia* varied with the different prey species the predator consumed. The duration of larval and pupal was 10.4 days when preying on *A. pomi*, 11.9 days on *A. glycines* and 13.9 days on *A. robiniae* (Dai, 1990). Veeravel and Baskaran (1996) determined the effect of temperature on growth and development of two commonly occurring coccinellids, *C. transversalis* and *M. sexmaculatus*. Patro and Behera (2000) recorded the larval duration of *M. discolor* to be 4.81±0.17 days when fed on *A. craccivora*. Semyanov (2001) reported the larval duration of *L. biplagiata* to be 16 days when *A. craccivora* was used as prey. Studies on the influence of temperature on the survival and development of immature stages revealed that the total larval period decreased significantly with increase in temperature from 20 to35\(^\circ\)C.
(Omkar and James, 2004b). Kalushkov and Hodek (2005) reported the larval duration of *P. quatordecimpunctata* to range from 8.4 to 9.1 days when reared on six aphid species. Devjani and Singh (2006) while studying the larval development and prey consumption of five aphidophagous predators in relation to two aphid species reported *C. transversalis* to be less affected by prey species offered in comparison to *C. septempunctata*. Suja and Beevi (2007) studied the biology and efficiency of *C. transversalis*, *H. octomaculata* and *M. sexmaculatus* on *A. craccivora*. Lokeshwari *et al.* (2010a) observed the pre-adult development of *M. sexmaculatus* when fed on two different densities of three aphid species viz., *A. craccivora*, *A. gossypii* and *M. persicae*. Pre-adult development was shortest (11.43±0.65 days) when fed on high density of *A. craccivora*. Santos-Cividanes *et al.* (2011) recorded a direct correlation between development time and feeding interval in *C. maculata* larvae. Krengel *et al.* (2012) investigated the effects of two daily temperature profiles during pre-imaginal development and young adult period on body weight and fat body content of adult *C. septempunctata* and *H. axyridis*. Majumder and Agarwala (2013) observed that the egg, larval, pre-pupal and pupal stages of *A. dilatata* lasted 4.73±0.08, 14.84±0.16, 2.13±0.03 and 6.58±0.10 days respectively.
2.2.3. Weight and relative growth rate

Weights of ladybeetles are controlled by environmental factors, nutrition, genes, sex and their activity patterns (Hodek, 1973; Wigglesworth, 1973; Phoofolo et al., 2008). An increase in the weight and survival with increasing daily availability of prey has been reported in *H. axyridis* (Hukusima and Ohwaki, 1972), *A. bipunctata* (Dimetry, 1976) and *P. japonica* (Kawauchi, 1979). Rhamhalinghan (1985) reported that the level of larval food consumption significantly affected not only the size and weight of *C. septempunctata* adults, but also the number of ovarioles. Ng (1991) concluded a direct correlation between feeding rate in *C. sexmaculata* larvae with the weight of emerged adults. However, in certain cases additional food consumption did not contribute to the weight of the adults (Smith, 1965). Weight of newly eclosed adults of *Cycloneda ancoralis* differed significantly when fed on different aphids. Variations in weights were also recorded between sexes, where females weighed more than males (Elliot et al., 1994; Omkar et al., 2005). Sugiura and Takada (1998) observed the female pupae of *C. sexmaculata* to be significantly heavier when larvae were fed on *Aulacorthum solani* and *M. persicae* than on *A. pism* or *S. akebiae*. Isikber and Copland (2001) observed the pre-pupa to be heavier than pupa owing to biochemical changes during metamorphosis. Omkar and Srivastava (2002) reported that life stages of *C.*
C. septempunctata weighed heaviest when reared on *L. erysimi*. The weights of different larval instars of *C. sexmaculata* were significantly influenced by the prey species they consumed and heaviest weights of larvae were recorded when reared on *A. craccivora* (Omkar and Bind, 2004). Bilashini et al. (2006) while assessing the performance of *C. septempunctata* larvae to varying prey densities observed the larval weight to be maximum at the density of 45 aphids which declined thereafter. Phoofolo et al., (2008) observed that weight of larvae of three coccinellid species was significantly affected by food deprivation period.

The relative growth rate in the present context refers to the conversion of aphid prey to coccinellid predator biomass and it generally increases with an increase in availability of food. Dixon (2000) reported that the relative growth rates of female *A. bipunctata* were higher than male larvae. Omkar and Srivastava (2003c) evaluated the prey quality dependent growth of *C. septempunctata* on six prey species and observed that the relative growth rate was maximum when fed on *L. erysimi* followed by *M. persicae, A. craccivora, A. gossypii, U. compositae* and *A. nerii*. Soares et al. (2004) found that relative growth rate of male and female *H. axyridis* did not differ significantly when ladybeetles were fed on mixed diet of *M. persicae* and *A. fabae*. Studies on relative growth rate of larvae depending on the prey species consumed have also been conducted for *C. sexmaculata*
Devi et al. (2007) observed the relative growth rate of *C. transversalis* at low and high aphid density of *A. craccivora*. Saengyot and Burikam (2012) studied the growth ratio of *Sasajiscymnus quinquepunctatus* (Weise).

### 2.2.4. Food conversion efficiency

Food conversion efficiency or efficiency of conversion of ingested food (ECI) is the percentage of consumed prey biomass converted into predator biomass (Waldbauer, 1968). ECI was found to vary with food conditions so as to reduce the adverse effect of food shortage. Food conversion rates of *A. bipunctata* larvae consuming *Sitobion avenae* increased to 34.40% from 22-29% when the predator received a reduced number of aphids, only 25% of what larvae ate when they were offered aphids *ad libitum* (Schuder et al., 2004). Similar rates of increase of ECI at low levels of food consumption had also been reported in *C. sexmaculatus* (Agarwala and Bardhanroy, 1997), *C. transversalis* (Devi et al., 2007). Omkar and Pervez (2004) recorded that ECI in terms of eggs laid in *P. dissecta* decreased with increase in prey density. Agarwala and Bardhanroy (1997) concluded that decrease in ecological growth efficiency at high food level could be due to the combined effects of satiation and lower rates of ingestion at higher food density. Aphidophages thus apparently feed with
less than full efficiency of conversion at high prey levels, though the fitness benefits are not yet clear (Dmitriew and Rowe, 2007).

Food conversion rates of ladybirds also vary for a given prey depending on the age of the predator, the morph of the prey and the host plant on which the prey feeds. Isikber and Copland (2001) reported that fourth instars of *S. levaillanti* and *C. sanguinea* feeding on *A. gossypii* had lower ECIs than earlier instars. Contrary to the above observation, Satpathi (2000) and Navodita and Ashwani (2011) reported that ECI increased from first instar larvae to fourth instar larval stage. Higher egg production by *H. convergens* feeding on apterous virginoparous nymphs of *M. persicae* compared to alatiform gynoparous was reported by Wipperfuerth *et al.*, (1987). Shannag and Obeidat (2006) found a higher ECI (19% dry weight basis) throughout the larval period of *C. septempunctata* when feeding on *A. fabae* from susceptible *Vicia faba* when compared with an ECI of 14% on aphids from a resistant cultivar.

ECIs also differ between ladybird species depending on their nature of feeding and type of prey. In general, ECIs depend both on the predator’s ability to digest and assimilate consumed food (Jalali *et al.*, 2009a, b; Lundgren, 2009) and on the allocation of the assimilated nutrients towards maintenance, growth and activities such as foraging and reproduction (Agarwala *et al.*, 2008; Kajita *et al.*, 2009). Both consumption and
assimilation efficiency, measured as ratio of weight of faeces produced to weight of aphids consumed decreased along with egg production in females of *M. sexmaculatus, C. transversalis* and *H. axyridis* (Dixon and Agarwala, 2002). The improved ability of ladybirds to grow and reproduce given a selection of different prey is likely to include increased assimilation as well as consumption of prey (Rana *et al.*, 2002).

### 2.3. REPRODUCTIVE FITNESS IN COCCINELLIDS

The reproductive behavior of an organism and its various aspects maximize the chances of survival of future generation. A considerable amount of work has been done to study the oviposition behavior in ladybirds (Agarwala *et al.*, 1988; Honek and Hodek, 1996; Omkar and Singh, 2010; Nedved and Honek, 2012). Reproductive performance of aphidophagous coccinellid predators are known to depend largely on their food quality as well as quantity.

#### 2.3.1. Age and size of females at maturity

The response of age at maturity to changes in an individual’s growth conditions is one of the frequently studied traits (Berringan and Charnov, 1994; Day and Rowe, 2002). Age at maturity determines how quickly individuals in a population can start to reproduce and how much they can reproduce (Roff, 1992). Various results show that a wide range of response
of age to changes in individual’s growth condition is possible (Stearns and Koella, 1986; Berring and Koella, 1994; Day and Rowe, 2002). In general, most organisms mature earlier as growth conditions improve (Gotthard and Nylin, 1995). However, many animals fail to mature till a minimum size is attained which generally happens under poor growth conditions. Day and Rowe (2002) suggested that variation in food availability impact ladybirds in terms of their size and age at maturity and fecundity which is important in understanding their ecology and biocontrol potential. Besides, temperature (Atkinson, 1994), growth rate (Berringan and Charnov, 1994), risk of predation (Ball and Becker, 1996) and time of season (Nylin et al., 1989; Johansson et al., 2001) have been reported to have significant influence on the age and size at maturity. Agarwala and Bhoumik (2011) also studied the effect of resource gradient on age and size at maturity in H. axyridis.

Ladybirds vary in size both within and between species and between sexes within a species (Dixon, 2000). Size is a consequence of the relative effect of food quantity and temperature on the growth and developmental rates. Kindlmann and Dixon (1992) assumed that these relationships were shaped by selection and the resultant variation in adult size within a species is a consequence of maximizing the population growth rate, \( r_m \). Larval development on low food supply significantly affected the size, survival to
adulthood and reproduction of adults (Kaddou, 1960; Smith, 1965; Kawauchi, 1990; Ng, 1991; Pereyra and Archangelsky, 2007; Losey et al., 2012). Crowding during larval development has also been reported to result in decreased size of adults (Omkar and Pathak, 2009). Further, Riddick and Wu (2012) concluded that quality of prey consumed by *Stethorus punctillum* during larval stage can affect their size as adults and consequently the size of their eggs. Size differences in adult predaceous ladybirds are also common in nature (Hodek and Honek, 1996) with smaller size ladybirds occurring frequently in fields (Obrycki et al., 1998). This reinforces the prediction that beetles often live in habitats that are limited by food supply (Dixon, 1997). Also, size of predators have often been correlated with many determinants of fitness such fecundity (Honek, 1993), survival (Savage et al., 2004) and ability to secure resources such as prey (Menge, 1972) and mates (Howard et al., 1997).

2.3.2. Reproductive duration and fecundity

Reproductive duration or oviposition period and fecundity are good measure of individual fitness. Reproductive duration refers to the duration of period between the first and the last egg batch while fecundity refers to the total number of eggs laid by female during its lifetime. Both these traits are species-specific and have been known to be influenced by temperature and quantity and quality of food during the pre-imaginal development of the
female and reproduction. Besides, fecundity is also influenced by mating frequency, mating duration, age of parents, population density, illumination, photoperiod, phenotype and with generation (Nedved and Honek, 2012).

The length of reproductive period and fecundity varied with temperature. Reproduction in *L. biplagiata* is independent of photoperiod even at $20^0C$ and ovogenesis ceases at low temperature in the range of 10 to $15^0C$. Mean fecundity was found to be $1064 \pm 96$ eggs with minimum of 690 and maximum of 1229 eggs per female (Semyanov and Bereznaja, 1988). Fecundity and longevity of *Cryptolaemus montrouzieri* was greatly affected by lower and higher temperature and also by age of the female (Jalali *et al.*, 1999). Uygun and Atlıhan (2000) studied the effect of temperature on development and fecundity of *Scymnus levallanti*. In *M. discolor*, fecundity was lowest at $20^0C$, highest at optimum temperature and decreased at $30^0C$ (Omkar and Pervez, 2002a). Srivastava and Omkar (2003) studied the influence of temperature on certain biological attributes of *C. septempunctata* and found that percent hatching, fecundity and oviposition period were highest at $30^0C$. Omkar and James (2004b) reported that fecundity of *C. transversalis* ranged between 370.6 to 1319.8 eggs depending on temperatures with optimum at $27^0C$. The oviposition period of *Anisoscymnus cardilobus* lasted for 109, 61 and 17 days at the temperature of $17^0$, $26^0$ and $32^0C$ respectively (Huang *et al.*, 2008).
Ponsonby (2009) reported that in *Chilocorus nigritus* the lifetime fecundity increased from 20 to $24^0C$ and then decreased at $30^0C$.

Hodek and Honek (1996) reported that food quality has a major influence on the intrinsic growth rate and reproductive rates of ladybirds. Agarwala *et al.* (1988) reported fecundity and oviposition period in *M. discolor* to vary with the prey species. Fecundity was higher for females fed on *A. craccivora*. The egg laying period in *C. saucia* ranged from 27 to 129 days and each female laid 213 to 1290 eggs depending on the aphid species they were fed (Dai, 1990). Agarwala and Yasuda (2000) observed variation in reproductive period of *C. sexmaculata* depending on aphid species used as food. Babu (2001) observed that egg laying by *C. sexmaculata* was significantly enhanced when fed upon adult aphid than nymphs. Oviposition period in *C. septempunctata* was recorded as 22.4 days when reared upon *S. avenae* (Rana and Kakker, 2000) which decreased to 16 days when reared upon *B. brassicae* (Elhag and Zaitoon, 1996). Influence of prey species on the growth and reproduction has also been studied in *C. septempunctata* (Omkar and Srivastava, 2003c), *C. sexmaculata* (Omkar and Bind, 2004), *C. transversalis* (Omkar and James, 2004a), *P. quatourdecimpunctata* (Kalushkov and Hodek, 2005), *A. bipunctata* (Ferrer *et al*., 2008), *A. cardoni* (Omkar *et al*., 2009), *A. variegata* and *C. lunata* (Nyaanga *et al*., 2011).
Omkar and Pervez (2003a) studied the influence of prey deprivation on the biological attributes of *P. dissecta* and found that oviposition period, post-oviposition period, fecundity, viability of eggs and longevity of females significantly decreased with the increase in duration of prey deprivation. Study on the life-history responses of *H. axyridis* to food stress revealed a marked reduction in the reproductive period and fecundity of the coccinellid (Agarwala *et al.*, 2008). Furthermore, Santos-Cividanes *et al.* (2011) studied the effect of feeding interval on the development, survival, fecundity and longevity of *C. maculata*.

Numerical response is the increase in the number of predators either primarily by changes in their spatial distribution or secondarily by more intensive reproduction resulting from higher abundance of prey (Holling, 1965). A two-fold increase in prey density brought about a two-fold increase in the oviposition rate in *C. septempunctatata* (Xia *et al.*, 1999). Density dependent reproduction has also been studied in *M. sexmaculatus* and *C. transversalis* (Agarwala and Bardhanroy, 1997, 1999) and *H. dimidiata* (Sharmila *et al.*, 2009). Ponsonby and Copland (2007) observed that a decrease in prey density caused a significant but transient decline in egg production in *C. nigritus*.

Further, reproductive attributes in ladybirds was observed to be affected by the age of both male and female beetles (Mishra and Omkar,
2004; Omkar et al., 2006b, 2010a). Number of matings (Bind, 2007; Omkar and Singh, 2010; Omkar et al., 2010b) and mating duration (Omkar et al., 2006a; Zhou et al., 2012) were also found to have an influence on the oviposition and fecundity of coccinellids. Omkar and Pathak (2006) reported that females of *C. saucia* kept under long day photoperiod and under white light showed better reproductive performance than those placed under other photoperiods and wavelengths. Other factors such as temporary prey isolation (Evans and Dixon, 1986) and body size (Agarwala and Bardhanroy, 1999) also affected egg production.

**2.3.3. Fecundity schedule in coccinellids**

Studies on reproduction in insects have tended to assume that fecundity schedule is shaped mainly by survivorship and that fecundity is dependent on adult size (Ziolko and Kozlowski, 1983; Stearns, 1992). Williams (1974) opined that selection would favour individuals that invest more in early reproduction even when there is an adverse effect on their potential longevity. In insects, the age schedule of fecundity tends to be triangular (Dixon, 2000) and is dependent on food supply or quality (Kawauchi, 1981; Evans and Dixon, 1986) and temperature (Ponsonby and Copland, 1998; Pervez and Omkar, 2004). Kindlmann et al. (2001) published an energy partitioning model that predicts a triangular fecundity in insects shaped by senescence. Fecundity function is also known to be
influenced by wavelength (Omkar et al., 2005a) and photoperiod (Mishra & Omkar, 2005).

Dixon and Agarwala (2002) studied the fecundity function and ageing in three coccinellid species viz., *C. transversalis*, *C. sexmaculata* and *H. axyridis*. The age-specific scheduled fecundity of ladybirds in terms of complete oviposition cycle and diel pattern of oviposition were studied by Omkar et al. (2004) in *C. septempunctata*, *C. transversalis* and *P. dissecta*. Srivastava and Omkar (2005) observed variations in the reproductive schedule of two morphs of *C. septempunctata*.

### 2.3.4. Hatching success

The percentage hatching of eggs or egg viability was reported to be maximum at certain optimum temperature, above or below which a reduction in the hatchability was noticed (Frazer and McGregor, 1992; Miller and Lamana, 1995; Lombaert et al., 2008). Ponsonby and Copland (1998) surmised that reduced viability in egg at low temperature was perhaps due to inhibition of spermatogenesis or sperm mortality in the spermathecae of females. Ng (1991) reported hatching percent of eggs to be influenced by the quality of aphids provided as prey. The greater amount of consumption of preferred prey increased the weight of eggs, which contained a large quantity of yolk and consequently increased egg hatching
(Simmons, 1988). Francis et al. (2001) inferred that increased levels of glucosinates in host plant deteriorated the quality of aphid prey, *M. persicae* which resulted in reduced egg viability in *A. bipunctata*. Dixon and Agarwala (2002) reported that early in reproductive life, *M. sexmaculatus* lays proportionately 1.4 times more fertile eggs than it lays towards the end of its life. Effect of parental age on the percent viability of egg has been well illustrated in *C. septempunctatata* and *P. dissecta* (Srivastava and Omkar, 2004; Pervez et al., 2004). Omkar and Mishra (2005) analyzed the costs and benefits involved in mating in aphidophagous ladybirds and found a relationship between hatching success and multiple mating. While studying the reproductive behaviour of *C. sexmaculata*, Bind (2007) also observed an increase in egg hatchability as a result of multiple mating. Majumder and Agarwala (2013) observed the hatching success of eggs laid by *A. dilatata* when reared on *C. silvestrii* to be 74.2%.

### 2.3.5. Adult longevity

Longevity in coccinellids has been reported to vary from one month to approximately three years (Milevoj, 1997). A long inactive period exists in certain species of coccinellids due to which their longevity extends beyond a year (Hodek and Honek, 1996). Longevity of ladybeetles has been reported to differ among sexes with female beetles having longer life-span (Hukusima and Kouyama, 1974; Omkar and Srivastava, 2002; Omkar and
James, 2004; Majumder and Agarwala, 2013) than males. This may be attributed to relatively lesser aphid consumption by males (Ryoo, 1996). Further, longevity has been found to be influenced by temperature (Chakrabarti et al., 1995; Huang et al., 2008), prey quality and quantity (Babu, 1999; Omkar and James, 2004a; Kalushkov and Hodek, 2005; Ponsonby, 2009; Pandi et al., 2012) and number of matings (Omkar and Mishra, 2005; Omkar et al., 2010b).

2.4. EFFECTS OF INTERACTION BETWEEN DIFFERENT PREDATOR SPECIES COMPETING FOR THE SAME PREY RESOURCE

A guild is a group of species in a community that share similar resources (food or space) regardless of difference in tactics of resource acquisition and in taxonomic position (Polis et al., 1989). Cannibalism and intraguild predations (IGP) are complex interactions that occur in biological communities and they constitute important determinants of population dynamics and community structure (Polis et al., 1989; Polis and Holt, 1992; Omkar et al., 2002). These interactions within and between niche-partitioning predators has evolved as a major research topic in biological control and conservation ecology and are highly prevalent in guild of insect predators, especially ladybirds (Agarwala and Dixon, 1991; Rosenheim et al., 1995; Yasuda and Shinya, 1997; Burgio et al., 2002; Agarwala et al.,
Intraguild predation (IGP) is defined as the killing and consumption of a species that uses similar resources and therefore a potential competitor (Felix and Soares, 2004). IGP includes (i) effective IGP where prey is killed and consumed, (ii) interspecific killing in which prey is killed but not consumed and (iii) IGP risk where prey is at risk of being killed and/or consumed (Lucas, 2005). These interactions may affect the density (density-mediated traits) of the species or any morphological, physiological or behavioural traits (traits mediated effects) (Lucas, 2012). Besides, IGP also has significant benefits as they reduce competition and protect depleting food resource and provide immediate nutritional gain (Dixon, 2000; Snyder et al., 2000).

IGP involving coccinellids in natural situations has been documented when aphid prey density was low (Hironori and Katsuhiro, 1997; Musser and Shelton, 2003; Schellhorn and Andow, 1999) or high (Gardiner and Landis, 2007; Gagnon, 2010). In addition to resource availability, spatial and temporal factors affecting overlap of ladybeetle species determine the incidence of IGP (Cottrell, 2005). Intraguild predation is described by its intensity or probability of occurrence (Lucas, 2005), direction (mutual or unidirectional) and symmetry (dominance or not of a species). The intensity of the interaction (Hindayana et al., 2001) as well as its direction (Frechette et al., 2007) changes according to complexity and size of the experimental
arena. Felix and Soares (2004) characterized and compared the magnitude, direction and symmetry of IGP between the developmental stages of the aphidophagous *H. axyridis* and *C. undecimpunctata* and concluded that mobility and body weight were the main factors affecting the magnitude of IGP. In ladybird beetles, large species usually eat small species resulting in asymmetrical interactions between two species (Obrycki et al., 1998). However in some cases, smaller species (*A. bipunctata*) may prove more toxic to large species (*C. septempunctata*) thereby reducing the incidence of small species being eaten by the large species (Hemptinne et al., 2000a).

Also, as intraguild predators, coccinellids frequently have sub-lethal effects on intraguild prey. The presence of *H. axyridis* slowed *A. bipunctata* larval development at high extraguild prey density, whereas IGP by *H. axyridis* or by *C. septempunctata* occurred at low extraguild prey density (Kajita et al., 2000). Physical interference by both conspecific and heterospecific individual have been reported by several workers to cause a decrease in fecundity of adult coccinellids (Hemptinne and Dixon, 1991; Agarwala et al., 2003a; Mishra and Omkar, 2006; Soares and Serpa, 2007; Alhmedi et al., 2010; Sharmila et al., 2011) and weight gained by larvae (Hoogendoorn and Heimpel, 2004; Sharmila et al., 2011). Presence of larval residues also deterred coccinellids from ovipositing (Hemptinne et al., 1993; Yasuda et al., 2000; Agarwala et al., 2003b; Michaud and Jyoti, 2007) and foraging (Meisner et al., 2011).
Larval and egg cannibalism represents a survival strategy for coccinellids under prey scarcity (Kindlmann and Dixon, 1993; Dixon, 2000) and it confers both nutritional and competitive advantages (Snyder et al., 2000; Gagne et al., 2002). Agarwala and Dixon (1993) suggested larval cannibalism as a function of relative vulnerability and frequency of encounters. However, a recent study on different components of cannibalism on three ladybird species viz., *H. axyridis, C. sanguinea* and *Olla v-nigrum* revealed that it is largely dependent on the species, food availability, degree of relatedness, size disparity and larval density. These ladybird larvae also could complete development feeding on conspecific eggs or larvae (Michaud, 2003). The larvae of *H. axyridis, C. septempunctata brucki* and *A. bipunctata* completed their development on conspecific eggs but failed to do so when provided with heterospecific eggs (Sato and Dixon, 2004). Omkar et al. (2005b) reported that females of both *P. dissecta* and *C. transversalis* were more reluctant to feed on heterospecific eggs than fourth instar larvae. Several authors suggested that eating heterospecific eggs may slow the predators’ development, decrease larval weight gain, adult size and even cause death (Phoofolo and Obrycki, 1998; Hemptinne et al., 2000a, b; Cottrell, 2004; Rieder et al., 2008). Slogett and Davies (2010) reported that the extent of egg predation depends on the defensive alkaloids present in eggs on individual species. Jafari (2013) while studying cannibalism in *H. variegata* under laboratory conditions observed that cannibalism rate was dependent on developmental stages.