International Journal of Tropical Insect Science (2019) 39:107–114
https://doi.org/10.1007/s42690-019-00006-9

ORIGINAL RESEARCH ARTICLE

Oviposition in aphidophagous ladybirds: effect of prey availability and conspecific egg presence

Shashwat Singh[1] · Geetanjali Mishra[1] · Omkar[1]

Accepted: 17 January 2019 / Published online: 9 May 2019

Abstract

Oviposition site selection in ladybirds is a dynamic process influenced by a number of abiotic and biotic factors. In this study we investigated whether prey quantity and egg presence (varying in relatedness and age) influence oviposition behavior in the zigzag ladybird, *Menochilus sexmaculatus* (Fabricius). Influence of these factors on cannibalism by females was also investigated and we tried to observe whether cannibalism was a modifying mechanism during oviposition site selection. Females were placed in prey abundant or scarce conditions in presence of related or unrelated eggs of varying ages, and their oviposition (for 24 h), egg viability and cannibalism were recorded. Prey-scarce conditions significantly decreased oviposition but had no influence on egg viability. Prey scarcity also increased the incidence of cannibalism by females. Females avoided laying eggs in the presence of related eggs regardless of their age. On the other hand, cannibalism was more in related eggs that were older in age. This increased cannibalism in presence of older related eggs, may be a comprehensive way of eliminating potential competition threats from a potential oviposition site already having eggs. All the independent factors (prey quantity, egg relatedness and egg age) did not affect egg viability, is the suggestive of male nutritional status rather than female.

Keywords Cannibalism · Coleoptera · Coccinellidae · Predator prey interaction

Introduction

Oviposition in ladybirds (Coleoptera: Coccinellidae) is influenced by a number of prevailing abiotic (Wang et al. 2013; Papanikolaou et al. 2013; Singh et al. 2018) and biotic (Seagraves 2009; Omkar et al. 2009; Bista and Omkar 2013; Tang et al. 2013) factors. It is essential for the females to select oviposition sites, taking into accord a multitude of factors, since egg being an immobile stage, is vulnerable to numerous dangers, like predation, parasitization, and pathogen infection (Dixon 2000; Seagraves 2009). A strong correlation between oviposition preference and offspring performance is supposed to be a strategy of the mother to enhance her inclusive fitness (Omkar and Mishra 2005).

Ladybirds select oviposition sites based on factors, such as (1) patch quality in terms of prey quantity (Hemptinne et al. 2000a; Fréchette et al. 2006; Oliver et al. 2006; Omkar et al. 2010), (2) age of aphid colony (Hemptinne et al. 2000a), (3) age of host plant (Seagraves 2009), (4) presence of larval tracks (Ruzicka 2006; Mishra et al. 2012, 2013), (5) physical presence of adults (Mishra and Omkar 2006), (6) cost of inter-patch movement in terms of energy and time, and (7) mortality risks to the offspring (Seagraves 2009). A few studies suggest that egg presence also modulates oviposition (Hemptinne and Dixon 1991; Mishra et al. 2012, 2013). In response to poor prey quantity and quality, ladybirds are known to either reduce oviposition (Oliver et al. 2006; Fréchette et al. 2006; Omkar et al. 2010; Barbosa et al. 2014; Santos et al. 2016; Singh et al. 2016), or completely avoid oviposition by resorbing their ovarioles (Osawa 2005; Kajita and Evans 2009; Ferrer et al. 2010) or search for further new patches for oviposition (Sloggett and Majerus 2000). In prey-scarce conditions, instead of avoiding such patches completely, ladybirds tend to lay extra non-viable eggs only for the purpose of nutrition, so as to provide for their viable eggs in the same egg batch (Perry and Roitberg 2005) and also for themselves (Santi and Maini 2007). Laying of trophic eggs as a source of nutrition is found in many animal groups, e.g. fishes (McKaye 1986), amphibians (Kam et al. 2000; Heying 2001; Gibson and Buley 2004),

✉ Omkar
omkaar55@hotmail.com

[1] Ladybird Research Laboratory, Department of Zoology, University of Lucknow, Lucknow 226007, India

insects (Frechette and Coderre 2000; Kudo and Nakahira 2001), spiders (Kim and Roland 2000; Kim and Horel 2000) and prosobranch snails (Baur 1992).

Poor prey conditions are also responsible for an increase in the incidence of cannibalism and intraguild predation (Takahashi 1989; Schellhorn and Andow 1999b; Dixon 2000; Cottrell 2005), with the former increasing more in ladybirds (Schellhorn and Andow 1999a; Hemptinne et al. 2000b, 2000c). This is probably owing to lesser chances of exposure to toxins in case of cannibalism (Burgio et al. 2002; Agarwala and Dixon 1992; Hemptinne et al. 2000b, 2000c). Sibling cannibalism in particular is suggested to have great adaptive significance in ladybirds by providing essential energy and nutrients, thereby accelerating development, increasing growth rate, and enhancing survival (Banks 1954, 1956; Kawai 1978; Roy et al. 2007). Sibling egg cannibalism is believed to have evolved under prey-scarce conditions due to fitness gains to both cannibals and victims (Osawa 1992).

While egg cannibalism is a more prevalent phenomenon, being an easy source of energy (Takahashi 1987; Agarwala and Dixon 1992), larval cannibalism has been investigated more in ladybirds (Michaud 2003; Pervez et al. 2006). In larval cannibalism, the role of size disparity (Yasuda et al. 2001), species specific context (Yasuda and Ohnuma 1999; Snyder et al. 2000), as well as kinship or relatedness (Michaud 2003; Pervez et al. 2005) have been observed. Results of these studies indicate a proclivity of smaller sized individuals and conspecifics to being cannibalized in prey-scarce conditions (Hodek et al. 2012). The few studies that have been undertaken on egg cannibalism in ladybirds, indicates the preference of conspecific eggs over heterospecific ones (Agarwala et al. 1998; Michaud 2002) with preference changing with the switching of egg surface chemicals (Omkar et al. 2004). This indicates the capability of discriminating between conspecifics and heterospecifics.

In view of the above facts on effect of prey scarcity on oviposition and cannibalism, we decided to assess the oviposition responses of female ladybirds under (a) prey-scarce and abundant conditions, and (b) presence of potential passive competitors in the form of previously laid conspecific eggs. While the prey scarcity condition is commonly found in nature owing to the ephemeral nature of aphids, the latter condition is more likely to occur in conditions of mass rearing or stock culture under laboratory conditions.

To address this we have varied prey density and egg presence to assess whether these factors modulated ladybird oviposition. Egg presence was varied in terms of age as well as relatedness, since the former signals the degree of danger of cannibalism in the future and the latter may have fitness consequences for the females. We hypothesize that in prey-scarce conditions, females will reduce their oviposition and percent egg viability. Secondly, females should lay fewer number of eggs in presence of related eggs. Lastly, we hypothesized that when females were placed in a constrained arena with conspecific eggs and no escape options, under prey-scarce conditions, they would cannibalize the older eggs as a nutrition source or to reduce competition as their hatching would danger the freshly laid eggs via cannibalism, and continue with oviposition. However, cannibalism would rarely happen under abundant prey conditions, while oviposition took place normally, as this prey density would be enough to support the life attributes. This study attempts to define the relationship between oviposition behavior and cannibalistic tendency of females in the presence of conspecific related and unrelated eggs of different ages.

To test these hypotheses, ladybird *Menochilus sexmaculatus* (Fabricius) (Coleoptera: Coccinellidae) was selected as the experimental model. It is a polymorphic ladybird beetle found abundantly almost throughout the year in area around Lucknow, India and feeds on a wide range of aphids (Omkar and Pervez 2004). Although studies related to reproductive biology have been conducted on this beetle (Omkar et al. 2006; Omkar and Bind 2007; Mishra et al. 2012, 2013), but there are no studies in the context of relatedness of eggs of different ages.

Materials and methods

Stock maintenance

Adults of *M. sexmaculatus* (30 males and 30 females) were collected from agricultural fields surrounding Lucknow, India (26° 50'N, 80°54′E). They were paired for mating in transparent plastic Petri dishes (9.0×2.0 cm^2) under laboratory conditions (27 ± 1 °C; $65 \pm 5\%$ R.H.; 14 L: 10D). They were provided with an ad libitum supply of pea aphid, *Acyrthosiphon pisum* (Harris) grown on broad bean, *Vicia faba* L. in polyhouse cultures (21 ± 1 °C; $65 \pm 5\%$ R.H. 14 L: 10D). Females were isolated post mating and provided with prey every 24 h. Eggs laid were separated and incubated under the above abiotic conditions until hatching. Larvae were reared until adult emergence in plastic beakers (14.5×10.5 cm^2; 5 larvae per beaker) under similar conditions as the parents. The adults for experiments were taken from the stock culture.

Experimental design

Unmated 15–20 day old females were monogamously paired with similar aged males in Petri dishes (9.0×1.5 cm^2) for 2 days in the presence of excess *A. pisum*. These multiply-mated females were then removed and placed in fresh Petri dishes for oviposition and shifted to a new Petri dish after every 1 h between 0700 and 1900 h with excess of *A. pisum*, regardless of whether they had oviposited or not, which helped determine the age of the eggs to the nearest hour for future experiments. From these, twenty eggs were randomly selected and remaining excess eggs, if any, were removed with the help of wet fine camel hair brush. Position of these selected twenty eggs was marked with a permanent marker and they were left for 12, 24 and 48 h, for further use in experiments.

We tested the combined effect of prey density, egg relatedness and egg age as factors affecting oviposition. For this, the Petri dishes containing eggs of different ages (12, 24 and 48 h) were first placed in two groups of either abundant (50 mg) or scarce (5 mg) prey conditions; these densities were decided on previous standardization experiments. Each egg age-prey group was further divided into two sub groups in which either the mother or an unrelated female of similar age was introduced (Fig. 1). After 24 h of these treatments, the females were removed. The number of fresh eggs laid, percent egg viability ([the number of eggs hatched/total number of eggs] ×100) of these eggs and cannibalism by mothers of marked eggs, if any, were recorded. Incidences of cannibalism, if any, were identified by observing for egg traces (remains of eggs) under stereoscopic binocular microscope (Magnus, Olympus India PVT. Ltd. Noida) at 16x magnification. In control treatments, females were provided with abundant or scarce prey conditions in absence of eggs. Similar observations were made. All treatments were conducted with 20 replicates.

Statistical analysis

All data were subjected to Kolmogorov-Smirnov test of normality and Bartlett's test of homogeneity of variances. Data were found to be normally distributed with equal variances.

Data obtained in experiment (presence of eggs of different ages at the two prey quantities) were first subjected to two-way ANOVA with prey quantity (abundant and scarce) and egg presence (no eggs [control] and egg presence [pooled data of different egg ages]) as independent factors; number of eggs laid by *M. sexmaculatus* females, percent egg viability and cannibalism by females were dependent factors followed by Tukey's post hoc comparison of means test at 5%.

Since significant difference of egg age was seen from control (presented in result section), the data were subjected to another ANOVA after removing the control data. In this, data on number of eggs laid, percent egg viability and number of eggs cannibalized by mothers were subjected to three-way ANOVA with amount of prey (abundant and scarce), egg relatedness (related or unrelated) and egg age (12, 24, 48 h) as independent factors followed by Tukey's post hoc comparison of means test at 5%. All statistical analyses were performed using MINITAB 15.0.

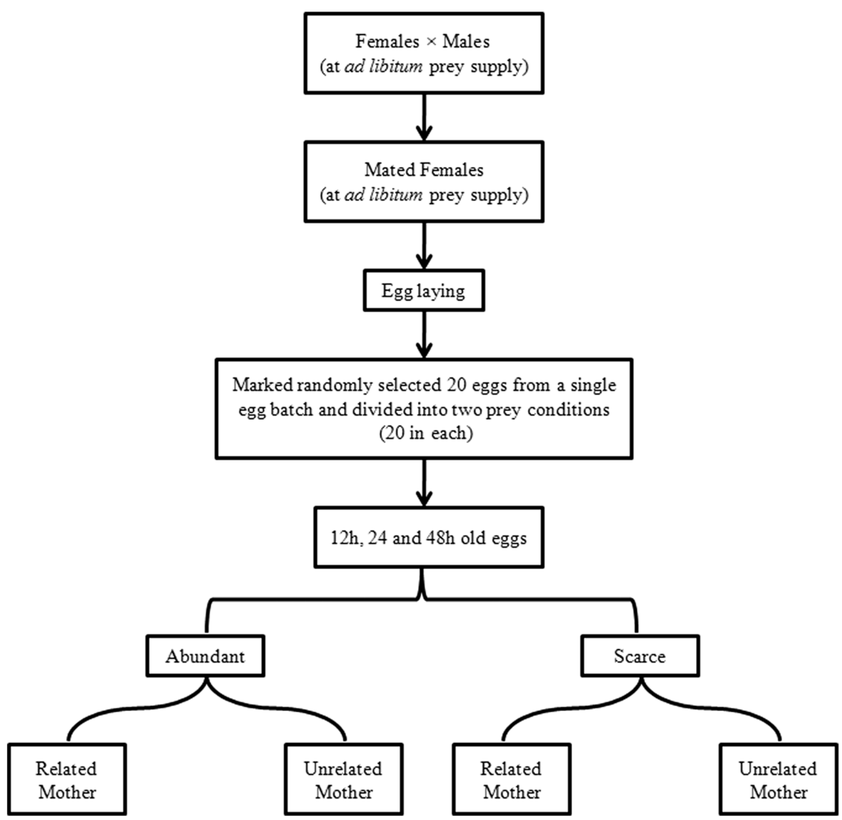

Fig. 1 Flow chart showing brief methodology of experiment

Results

Effect of prey quantity, egg relatedness and egg age on oviposition

Results of two-way ANOVA revealed that oviposition varied significantly with prey quantity ($F_{1,139} = 6995.34$, $P < 0.001$). Also, oviposition in control was significantly higher than the pooled egg age treatments ($F_{3,319} = 27.20$, $P < 0.001$). The interaction between both independent factors had insignificant effect ($F_{\text{prey quanity} \times \text{egg age } 3,319} = 1.45$, $P > 0.05$) on oviposition.

Since the effect of egg age was significantly different, the control was discarded and the remaining data (prey quantity, egg age and relatedness) were subjected to three-way ANOVA. Females of *M. sexmaculatus* oviposit significantly more eggs when provided with abundant prey ($F_{1,228} = 4782.697$, $P < 0.001$). In all egg age treatments, oviposition was significantly reduced in presence of eggs, either related or unrelated, in the presence of scarce or abundant prey ($F_{1,228} = 24.769$, $P < 0.001$) (Fig. 2). There was however no effect of egg age in any treatment ($F_{2,228} = 2.256$, $P > 0.05$). The interaction between prey quantity and egg relatedness was significant ($F_{\text{prey quantity} \times \text{egg relatedness } 1,228} = 4.071$, $P < 0.05$). However, the interactions, viz. $F_{\text{prey quantity} \times \text{egg age } 1,228} = 2.280$, $P > 0.05$; $F_{\text{egg relatedness} \times \text{egg age } 2,228} = 0.147$, $P > 0.05$; $F_{\text{prey quantity} \times \text{egg relatedness} \times \text{egg age } 2,228} = 2.081$, $P > 0.05$ were insignificant.

Effect of prey quantity, egg relatedness and egg age on percent egg viability

Initial ANOVA of pooled data revealed that percent egg viability was not significantly influenced by prey quantity ($F_{1,319} = 0.20$, $P > 0.05$) and egg age ($F_{3,319} = 0.32$, $P > 0.05$). The interaction between the two independent factors ($F_{\text{prey quantity} \times \text{egg age } 3,319} = 0.32$, $P > 0.05$) was also insignificant.

The subsequent three-way ANOVA after removing control data, revealed that there was insignificant effect of prey quantity ($F_{1,228} = 0.351$, $P > 0.05$), relatedness of eggs ($F_{1,228} = 0.310$, $P > 0.05$) and egg age ($F_{1,228} = 0.159$, $P > 0.05$) on percent egg viability. All interactions ($F_{\text{prey quantity} \times \text{egg relatedness } 1,228} = 0.004$, $P > 0.05$; $F_{\text{prey quantity} \times \text{egg age } 1,228} = 0.343$, $P > 0.05$; $F_{\text{egg relatedness} \times \text{egg age } 2,228} = 0.146$, $P > 0.05$; $F_{\text{prey quantity} \times \text{egg relatedness} \times \text{egg age } 2,228} = 0.067$, $P > 0.05$) had insignificant influence on percent egg viability (Fig. 3).

Effect of prey quantity, egg relatedness and egg age on cannibalism by females

Initial analysis of data revealed that cannibalism was significantly affected by prey quantity ($F_{1,319} = 101.82$, $P < 0.001$), egg age ($F_{3,319} = 48.54$, $P < 0.001$) and their interactions ($F_{\text{prey quantity} \times \text{egg age } 3,319} = 15.05$, $P < 0.001$).

The subsequent three-way ANOVA revealed that cannibalism varied significantly with prey quantity ($F_{1,228} = 102.934$, $P < 0.001$), egg relatedness ($F_{1,228} = 6.179$, $P < 0.05$) and egg age ($F_{2,228} = 4.869$, $P < 0.05$). Cannibalism was significantly higher in prey-scarce conditions, with related eggs and older eggs being cannibalized significantly more in prey-scarce conditions (Fig. 4) but not in prey abundant conditions (Fig. 4). While interaction between prey quantity and egg age was significant ($F_{\text{prey qauntity} \times \text{egg age } 1,228} = 4.251$, $P < 0.05$), the rest of the interactions were insignificant ($F_{\text{prey quantity} \times \text{egg relatedness } 1,228} = 2.199$, $P > 0.05$; $F_{\text{egg relatedness} \times \text{egg age } 2,228} = 0.018$, $P > 0.05$; $F_{\text{prey quantity} \times \text{egg relatedness} \times \text{egg age } 2,228} = 0.077$, $P > 0.05$).

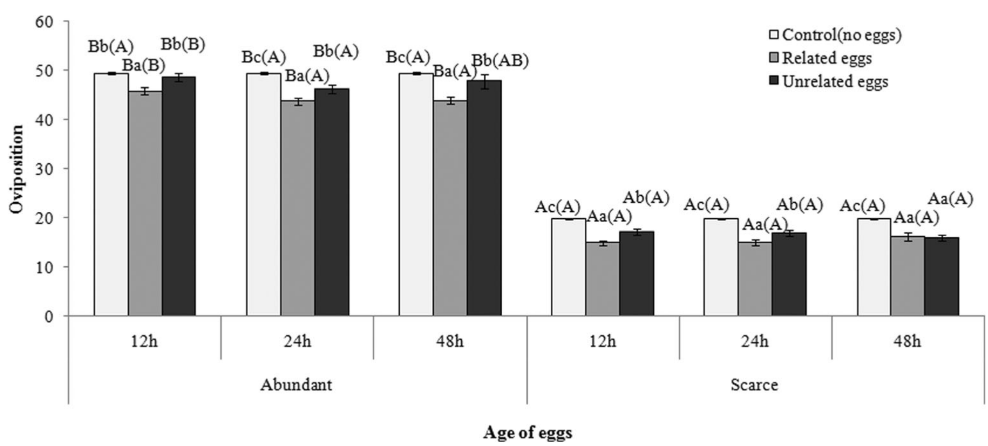

Fig. 2 Oviposition by *M. sexmaculatus* in the presence of different age eggs under abundant and scarce prey conditions. Values are mean ± SE. Large letters represent comparison of means between abundant and scarce prey conditions. Small letters represent comparison of means between egg relatedness treatments. Large letters in parenthesis represent comparison of means between egg age. Similar letters indicate lack of significant difference at $P > 0.05$

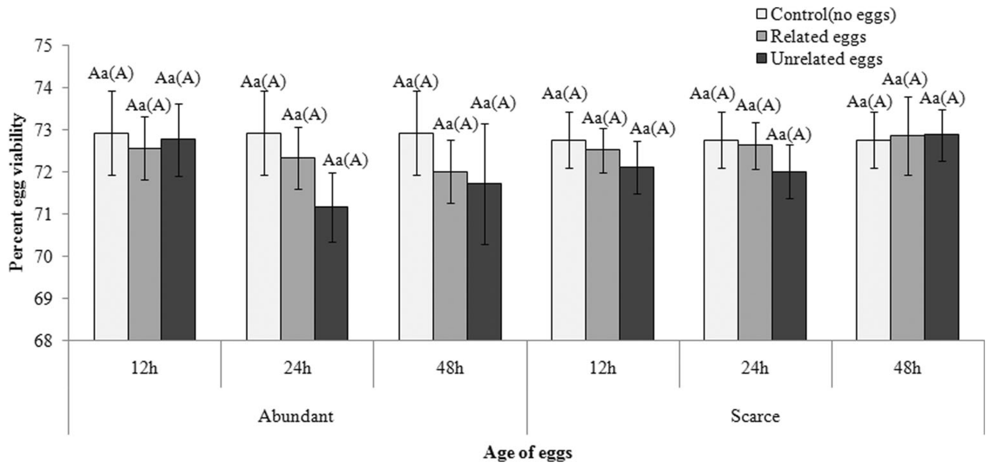

Fig. 3 Percent egg viability of *M. sexmaculatus* in the presence of different age eggs under abundant and scarce prey conditions. Values are mean ± SE. Large letters represent comparison of means between abundant and scarce prey conditions. Small letters represent comparison of means between egg relatedness treatments. Large letters in parenthesis represent comparison of means between egg age. Similar letters indicate lack of significant difference at $P > 0.05$

Discussion

Our results reveal that oviposition as well as cannibalism by females was influenced by combined effect of prey quantity, egg relatedness and egg age. As predicted in our hypothesis, females of *M. sexmaculatus* oviposited less in prey-scarce conditions. Such an expected decrease in oviposition with decrease in prey quantity has been reported in ladybirds, *Coccinella septempunctata* L. (Xia et al. 1999) and *Anegleis cardoni* (Weise) (Omkar et al. 2010). This phenomenon is easily explained through reduced availability of nutrients in general and non-availability of significant dietary proteins in particular, which assist in oogenesis or chorion development, as observed in seed beetle, *Stator limbatus* (Horn) (Fox et al. 1996), *Callosobruchus maculatus* (F.) (Cope and Fox 2003) and pentatomid bug, *Podisus nigrispinus* (Dallas) (Lemos et al. 2001). Resorption of eggs under prey-scarce conditions in anticipation of prey abundant conditions in the future as has been reported in the butterfly *Speyeria mormonia* (Boisduval) (Boggs and Ross 1993).

However, the percent egg viability was not influenced by prey-scarce conditions. The males in our study had not been kept in prey-scarce conditions thus indicating that percent egg viability is influenced by male nutritional status and not by female nutritional status. Such influence of males on egg viability in ladybirds is supported by earlier studies (Omkar et al. 2004; Pervez et al. 2004; Michaud et al. 2013). In fact we have observed in another study that if eggs of a single clutch of

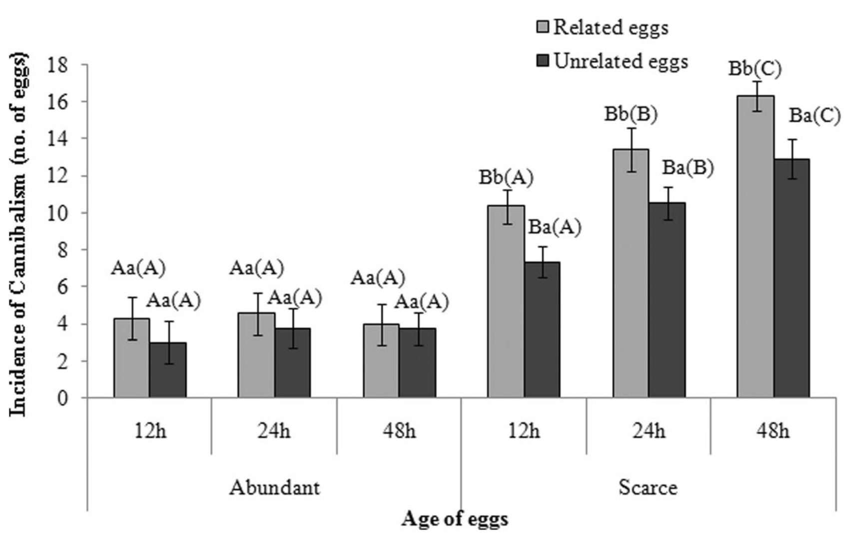

Fig. 4 Egg cannibalism by *M. sexmaculatus* in the presence of different age eggs under abundant and scarce prey conditions. Values are mean ± SE. Large letters represent comparison of means between abundant and scarce prey conditions. Small letters represent comparison of means between egg relatedness treatments. Large letters in parenthesis represent comparison of means between egg age. Similar letters indicate lack of significant difference at $P > 0.05$

M. sexmaculatus are separated and kept singly to prevent cannibalism, then around hundred percent hatching occurs.

The deterrent effect of related egg on oviposition by the ladybird is in support of our hypothesis and is probably a means of reducing the chances of cannibalism from close relatives. This behavior probably decreases the likelihood of competition between one's own offspring, thereby indirectly enhancing fitness. Discrimination between conspecifics and heterospecifics (Yasuda et al. 2001; Yasuda and Ohnuma 1999) as well as in kin (Pervez et al. 2005; Joseph et al. 1999) during larval cannibalism has been observed. Mishra et al. (2012) have also reported oviposition avoidance in presence of conspecific eggs, but they did not check for relatedness. The ability to recognize self and non-self in ladybirds has been reported (Pervez et al. 2005) and sibling egg cannibalism is probably more beneficial for females as they are more resource sensitive (Michaud and Grant 2004). Swapping of egg infochemicals has indicated their role in differentiating between con- and heterospecifics (Hemptinne et al. 2000b; Omkar et al. 2004) but not amongst kin and non-kin in ladybirds. It is possible that such infochemicals might allow females to discriminate between related and unrelated eggs.

However, while females refrained from ovipositing in presence of related eggs, they consumed them significantly more than unrelated ones under prey-scarce conditions. It has been reported previously that ladybird females are likely to suffer less loss of inclusive fitness on consumption of own eggs under prey-scarce conditions (Osawa 1992). Previous studies have shown the ability to discriminate and preferably consume conspecific eggs over heterospecific ones in some ladybirds (Hemptinne et al. 2000b; Michaud 2002) and such discrimination has been attributed to (i) similar surface alkanes, and (ii) presence of palatable and nutritious alkaloids in conspecifics. While a couple of studies have shown discrimination ability amongst kin and non-kin (Agarwala and Dixon 1993; Pervez et al. 2005), the mechanism of discrimination is yet to be elucidated.

Not only related but older eggs were cannibalized more. The increased consumption of older eggs by the ovipositing females may be ascribed primarily to removal of an immediate threat to her offspring, since they are more likely to cannibalize the eggs of the female post hatching. The preference for the consumption of older eggs (24 and 48 h) by the ladybird females has also been reported (Timms and Leather 2007). But this discrimination against older eggs during cannibalism did not extend to oviposition, which was similar in the presence of eggs of all ages.

Our study thus establishes that ladybirds are able to modulate their oviposition in response to prey quantity as well as relatedness of eggs in the vicinity, while at the same time not being influenced by the age of eggs. While the females seem to be able to discriminate amongst sites in their search for suitable oviposition sites, they probably additionally make their sites even more suitable by cannibalism of previously laid eggs, especially the older ones. The cannibalism of their own eggs under prey-scarce conditions seems to be a survival strategy. Also of interest in this study, it was shown that percent egg viability is not influenced by female nutritional status, but by male nutritional and ecological status.

Acknowledgements Shashwat Singh is thankful to University Grants Commission, New Delhi, India for BSR fellowship. Other authors are thankful to the Department of Higher Education, Government of Uttar Pradesh, Lucknow, India for providing financial assistance under the Centre of Excellence programme.

References

Agarwala BK, Dixon AFG (1992) Laboratory study of cannibalism and interspecific predation in ladybirds. Ecol Entomol 17:303–309

Agarwala BK, Dixon AFG (1993) Kin recognition: egg and larval cannibalism in *Adalia bipunctata* (Coleoptera: Coccinellidae). Eur J Entomol 90:45–50

Agarwala BK, Bhattacharya S, Bardhanroy P (1998) Who eat whose eggs? Intra- versus inter-specific interaction in starving ladybird beetles predaceous on aphids. Ethol Ecol Evol 10:361–368

Banks CJ (1954) The searching behaviour of coccinellids larvae. British J Anim Behav 2:37–38

Banks CJ (1956) Observations on the behaviour and mortality in Coccinellidae before dispersal from egg-shells. Proc Royal Entomol Soc 31:56–60

Barbosa PRR, Oliveria MD, Giorgi JA, Silva-Torres CSA, Torres JB (2014) Predatory behavior and life history of *Tenuisvalvae notata* (Coleoptera: Coccinellidae) under variable prey availability conditions. Fla Entomol 97(3):1026–1034

Baur B (1992) Cannibalism in gastropod. Cannibalism: ecology and evolution among diverse taxa. (ed. by M.A. Elgar and B.J. Crespi), pp 102-127. Oxford University Press, Oxford

Bista M, Omkar (2013) Effects of body size and prey quality on the reproductive attributes of two aphidophagous Coccinellidae (Coleoptera) species. Can Entomol 145, 566–576

Boggs CL, Ross CL (1993) The effects of adult food limitations on life history traits in *Spyeria mormonia* (Lepidoptera: Nymphalidae). Ecology 74:433–441

Burgio G, Santi F, Maini S (2002) On intra-guild predation and cannibalism in *Harmonia axyridis* (Pallas) and *Adalia bipunctata* L. (Coleoptera: Coccinellidae). Biol Control 24:110–116

Cope JM, Fox CW (2003) Oviposition decision in the seed beetle *Callosobruchus maculates* (Coleoptera: Bruchidae): effects of seed size on superparasitism. J Stored Prod Res 39:355–365

Cottrell TE (2005) Predation and cannibalism of lady beetle eggs by adult lady beetles. Biol Control 34:159–164

Dixon AFG (2000) Insect predator-prey dynamics: ladybird beetles and biological control. Cambridge University Press, Cambridge

Ferrer A, Dixon AFG, Gibernan G, Hemptinne JL (2010) Ovarian dynamics and specialisation in ladybirds. Ecol Entomol 35:100–103

Fox CW, Martin JD, Thakur MS, Mousseau TA (1996) Clutch size manipulation in two seed beetles consequences for progeny fitness. Oceologica 108:88–94

Frechette B, Coderre D (2000) Oviposition strategy of the green lacewing *Chrysoperla rufilabris* (Neuroptera: Chrysopidae) in response to extraguild prey availability. Eur J Entomol 97:507–510

Fréchette B, Dixon AFG, Alauzet C, Boughenou N, Hemptinne JL (2006) Should aphidophagous ladybirds be reluctant to lay eggs in the presence of unsuitable prey? Entomol Exp Appl 118:121–127

Gibson RC, Buley KR (2004) Maternal care and obligatory oophagy in *Leptodactylus fallax*: a new reproductive mode in frogs. Copeia 2004:128–135

Hemptinne JL, Dixon AFG (1991) Why ladybirds have generally been so ineffective in biological control?, pp. 149-447. In: Polgar L, Chamber RJ, Dixon AFG, Hodek I (eds) *Behavior and Impact of Aphidophaga*. SPB academic publishing, the Hauge

Hemptinne JL, Doumbia M, Dixon AFG (2000a) Assessment of patch quality by ladybirds: role of aphid and plant phenology. J Insect Behav 13:353–359

Hemptinne JL, Lognay G, Gauthier C, Dixon AFG (2000b) Role of surface chemical signals in egg cannibalism and intraguild predation in ladybirds (Coleoptera: Coccinellidae). Chemoecology 10:123–128

Hemptinne JL, Dixon AFG, Gauthier C (2000c) Nutritive cost of intraguild predation on eggs of *Coccinella septempunctata* and *Adalia bipunctata* (Coleoptera: Coccinellidae). Eur J Entomol 97: 559–562

Heying HE (2001) Social and reproductive behaviour in the Madagascan poison frog, *Mantella laevigata*, with comparisons to the dendrobatids. Anim Behav 61:567–577

Hodek I, Van Emden HF, Honek A (2012) Ecology and behavior of the ladybird beetles (Coccinellidae). A John Wiley and Sons, Ltd., Publication, U.K.

Joseph SB, Synder WE, Moore AJ (1999) Cannibalizing *Harmonia axyridis* (Coleoptera: Coccinellidae) larvae use endogenous cues to avoid eating relatives. J Evol Biol 12:792–797

Kajita Y, Evans EW (2009) Ovarian dynamics and oosorption in two species of predatory lady beetles (Coleoptera: Coccinellidae). Physiol Entomol 34:185–194

Kam YC, Chen YH, Chen TC, Tsai IR (2000) Maternal brood care of an arboreal breeder, *Chirixalus eiffingeri* (Anura: Rhacophoridae) from Taiwan. Behaviour 137:137–151

Kawai A (1978) Sibling cannibalism in the first instar larvae of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). Kontyu 46:14–19

Kim KW, Horel A (2000) Matriphagy in the spider *Amaurobius ferox* (Araneidae, Amaurobiidae): an example of mother offspring interactions. Ethology 104:1021–1037

Kim KW, Roland C (2000) Trophic egg laying in the spider, *Amaurobius ferox*: mother-offspring interactions and functional value. Behav Process 50:31–42

Kudo SI, Nakahira T (2001) Trophic egg production and its function in a subsocial cydnid bug. Adv Ethol 3:197

Lemos WP, Medeiros RS, Ramalho FS, Zanuncio JC (2001) Effects of 384 plant feeding on the development, survival and reproduction of *Podisus nigrispinus* (Dallas) (Hetroptera: Pentatomidae). Int J Pest Manage 47:89–93

McKaye KR (1986) Trophic eggs and parental foraging for young by the catfish *Bagrus meridionalis* of Lake Malawi, Africa. Oecologia 69: 367–369

Michaud JP (2002) Invasion of the Florida citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and asymmetric competition with a native species, *Cyclomeda sanguine*. Environ Entomol 31: 827–835

Michaud JP (2003) A comparative study of larval cannibalism in three species of ladybird. Ecol Entomol 28:92–101

Michaud JP, Grant AK (2004) Adaptive significance of sibling egg cannibalism in Coccinellidae: comparative evidence from three species. Ann Entomol Soc Am 97:710–719

Michaud J. P., Bista M., Mishra G. and Omkar (2013) Sexual activity diminishes male virility in two Coccinella species: consequences for female fertility and progeny development. Bull Entomol Res 103: 570–577

Mishra G, Omkar (2006) Conspecific interference by adults in an aphidophagous ladybird *Propylea dissecta* (Coleoptera: Coccinellidae) effects on reproduction. Bull Entomol Res 96:407–412

Mishra G, Singh N, Shahid M, Omkar (2012) Effect of presence and semiochemicals of conspecific stages on oviposition by ladybirds (Coleoptera: Coccinellidae). Eur J Entomol 109:363–371

Mishra G, Singh N, Shahid M, Omkar (2013) The effects of three sympatric ladybird species on oviposition by *Menochilus sexmaculatus* (Coleoptera: Coccinellidae). Chemoecology 23:103–111

Oliver TH, Timms JEL, Taylor A, Leather SR (2006) Oviposition responses to patch quality in the larch ladybird *Aphidecta obliterata* (Coleoptera: Coccinellidae): effects of aphid density, and con- and heterospecific tracks. Bull Entomol Res 96:25–34

Omkar, Bind (2007) Reproductive behavior of generalist aphidophagous ladybird beetle *Cheilomenes sexmaculata* (Coleoptera: Coccinellidae). Int J Trop Insect Sci 27:78–84

Omkar, Mishra G (2005) Preference-performance of a generalist predatory ladybird: A laboratory study. Biol Control 34:187–195

Omkar, Pervez A (2004) Predacious Coccinellids in India: predator-prey catalogue. Orient Insects 38:27–61

Omkar, Pervez A, Gupta AK (2004) Role of surface chemicals in egg cannibalism and intraguild predation by neonates of two aphidophagous ladybirds, *Propyela dissecta* and *Coccinella transversalis*. J Appl Entomol 128:691–695

Omkar, Pervez A, Gupta AK (2006) Why do neonates of aphidophagous ladybird beetles preferentially consume conspecific egg in presence of aphids. Biocontrol Sci Techn 16:233–243

Omkar, Sahu J, Kumar G (2010) Effect of prey quantity on reproductive and developmental attributes of a ladybird beetle, *Anegleis cardoni*. Int J Trop Insect Sci 30:48–56

Omkar, Kumar G, Sahu J (2009) Performance of a predatory ladybird beetle, *Anegleis cardoni* (Coleoptera: Coccinellidae) on three aphid species. Eur J Entomol 106:565–572

Osawa N (1992) Sibling cannibalism in the ladybird beetle *Harmonia axyridis* fitness consequence for mother and offspring. Popul Ecol 34:45–55

Osawa N (2005) The effect of prey availability on ovarian development and oosorption in the ladybird beetle *Harmonia axyridis* (Coleoptera : Coccinellidae). Eur J Entomol 102:503–511

Papanikolaou NK, Milonas PG, Kontodimas DC, Dermiris N, Matsinos YG (2013) Temperature dependent development, survival, longevity, and fecundity of *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). Ann Entomol Soc Am 106:228–234

Perry JC, Roitberg BD (2005) Ladybird mothers mitigate offspring starvation risk by laying trophic eggs. Behav Ecol Sociobiol 58:578–586

Pervez A, Gupta AK, Omkar (2005) Kin recognition and avoidance of kin cannibalism by the larvae of co-occurring ladybirds: a laboratory study. Eur J Entomol 102, 513–518

Pervez A, Gupta AK, Omkar (2006) Larval cannibalism in aphidophagous ladybirds: influencing factors, benefits and costs. Biol Control 38:307–313

Pervez A, Omkar, Richmond AS (2004) The influence of age on reproductive performance of a predatory ladybird beetle, *Propylea dissecta*. J Insect Sci 4:1–8

Roy HE, Rudge H, Goldrick L, Hawkins D (2007) Eat or be eaten: prevalence and impact of egg cannibalism on two-spot ladybirds, *Adalia bipunctata*. Entomol Exp Appl 125:33–38

Ruzicka Z (2006) Oviposition-deterring effects of conspecific and heterospecific larval tracks on *Cheilomenes sexmaculata* (Coleoptera:Coccinellidae). Eur J Entomol 103:757–763

Santi F, Maini S (2007) Ladybirds mothers eating their eggs: is it cannibalism? B Insectol 60:89–91

Santos EA, Costa PMG, Torres JB, Silva-Torres CSA (2016) Use of prey and non-prey food by the ladybird beetle *Eriopis connexa*

(Coleoptera: Coccinellidae) under laboratory rearing conditions. Biocontrol Sci Techn 26 (9):1184–1196

Schellhorn NA, Andow DA (1999a) Cannibalism and interspecific predation: role of oviposition behavior. Ecol Appl 9:418–428

Schellhorn NA, Andow DA (1999b) Mortality of coccinellids (Coleoptera: Coccinellidae) larva and pupae when prey become scarce. Popul Ecol 28:1092–1100

Seagraves MP (2009) Lady beetle oviposition behavior in response to the trophic environment. Biol Control 51:313–322

Singh S, Mishra G, Omkar (2016) Perceived prey quantity modulates oviposition in the ladybird *Menochilus sexmaculatus*. J Ethol 34: 59–64

Singh S, Mishra G, Omkar (2018) Plasticity in reproductive output and development in response to thermal variation in ladybird beetle, *Menochilus sexmaculatus.* J Therm Biol 71:180–188

Sloggett JJ, Majerus MEN (2000) Habitat preferences and diet in the predatory Coccinellidae (Coleoptera): an evolutionary perspective. Biol J Linn Soc 70:63–88

Snyder WE, Joseph SB, Preziosi RF, Moore AF (2000) Nutritional benefits of cannibalism for the lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae) when prey quality is poor. Environ Entomol 29:1173–1179

Takahashi K (1987) Cannibalism by the larvae of *Coccinella septempunctata bruckii* Mulsant (Coleoptera: Coccinellidae) in mass rearing experiments. Jpn J Appl Entomol Z 31:201–205

Takahashi K (1989) Intra- and inter-specific predations by lady beetles in spring alfalfa fields. Jpn J Entomol 57:199–203

Tang L, Wu J, Ali S, Ren S (2013) The influence of different aphid prey species on the biology and life table parameters of *Propylea japonica*. Biocontrol Sci Techn 6:624–636

Timms JEL, Leather SR (2007) Ladybird egg cluster size: relationships between species, oviposition substrate and cannibalism. Bull Entomol Res 97:613–618

Wang S, Tan XL, Guo NJ, Zhang F (2013) Effect of temperature and photoperiod on the development, reproduction, and predation of predatory ladybird *Cheilomenes sexmaculata* (Coleoptera: Coccinellidae). J Econ Entomol 106:2621–2624

Xia JY, Werf WVD, Rabbinge R (1999) Temperature and prey density on bionomics of *Coccinella septempunctata* (Coleoptera: Coccinellidae) feeding on *Aphis gossypii* (Homoptera: Aphididae) on cotton. Environ Entomol 28:307–314

Yasuda N, Ohnuma N (1999) Effect of cannibalism and predation on the larval performance of two ladybird beetles. Entomol Exp Appl 93: 63–67

Yasuda N, Kikuchi T, Kindlmann P, Sato S (2001) Relationship between attack and escape rates, cannibalism and intraguild predation in larvae of two predatory ladybirds. J Insect Behav 14:373–384