dominance of solitary over clustered fruiting habit, besides indicating bi-allelic monogenic inheritance of fruits node^{-1}. These results are in agreement with those of Gopalakrishnan *et al.*[7], Dhamayanthi and Reddy[8], and Stommel and Griesbach[9], who also reported monogenic control of fruits node^{-1} in chilli. Sergius[10] reported that multiple small fruits node^{-1} (a trait highly preferred by farmers of Western Africa) is dominant over solitary fruits node^{-1} in okra, and is controlled by a single biallelic gene.

The F$_1$s derived from parents contrasting for orientation of fruits produced pendant fruits, suggesting dominance of pendant over erect fruiting habit. The good fit of observed segregation with that expected (3P : 1E in F$_2$, 1P : 0E in B$_1$ and 1P : 1E in B$_2$ generations) (Table 4) confirmed the dominance of pendant over erect fruiting habit, besides suggesting bi-allelic monogenic inheritance of fruit orientation. However, Gopalakrishnan *et al.*[7] and Dhamayanthi and Reddy[8] reported that fruit orientation in chilli is controlled by a pair of dominant genes with inhibitory epistasis. Thus, it appears that the mode of action and number of genes controlling fruit orientation in chilli vary with genetic background of the material used to study the pattern of inheritance.

A good agreement between observed joint segregation of fruits node^{-1} and orientation of fruits in F$_2$, B$_1$ and B$_2$ generations derived from the crosses PJ × PC1, JL × CMS 10B and JL × CMS 8B involving parents which differed for both fruits node^{-1} and fruit orientation with that expected (9SP : 3SE : 3CP : 1CE in F$_2$, 1SP : 0SE : 0CP : 0CE in B$_1$ and 1SP : 1SE : 1CP : 1CE in B$_2$) (Table 5), suggested independent segregation of genes controlling the two fruiting habit traits.

Our results are of strategic importance in chilli-breeding research. Non-linkage of genes controlling fruits node^{-1} and orientation of fruits clearly suggests possibility of developing chilli cultivars with any desired combination of fruiting habit traits preferred by farmers. Further, both fruits node^{-1} and fruit orientation being simply inherited and visually assayable, could be used as diagnostic descriptor traits for identifying and eliminating duplicates and maintaining the identity of germplasm accessions; this is a daunting task, especially if they are in large numbers. The fruiting habit traits are also useful for the identification of true hybrids, and establishing distinctness, uniformity and stability of cultivars, a prerequisite for protecting intellectual property rights associated with the development of cultivars.

Solitary fruits node^{-1} and pendant fruit orientation are dominant over clustered fruiting and erect fruit orientation respectively. Fruits node^{-1} (solitary versus clustered) and orientation of fruits (pendant versus erect) are each controlled by single, bi-allelic, unlinked genes.

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Ladybird, *Menochilus sexmaculatus* (Fabricius) can survive on oophagy but with altered fitness than aphidophagy

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Egg consumption is common among insects, including ladybirds. The consumed eggs may be conspecific or heterospecific. Egg consumption eliminates potential competitors and provides additional nutrients for development and reproduction. In ladybirds, the incidence of cannibalism and intraguild predation has been proven as alternative tactics for the sustenance of life under prey-scarce condition. The consumption of conspecific eggs is known as cannibalism. Thus, in this study we have evaluated the effect of diets, viz. conspecific and heterospecific eggs along with aphids on egg consumption, developmental and reproductive attributes of a ladybird beetle, *Menochilus sexmaculatus* (Fabricius) (Coleoptera: Coccinellidae). We found that all the immature stages and adults prefer and

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consumed more conspecific eggs than heterospecific eggs possibly owing to low toxicity. Fourth instars and adult females consumed higher number of conspecific (82.15 ± 4.94 and 85.04 ± 0.05 respectively) and heterospecific eggs (56.61 ± 0.44 and 60 ± 0.48 respectively) than other life stages. Further the life stages developed faster on aphids followed by conspecific and heterospecific eggs. Besides aphids, overall maximum number of eggs was laid on conspecific eggs (84.00 ± 1.92) followed by heterospecific eggs (67.70 ± 1.07). However, reverse trend was observed for per cent egg viability. Thus, with scarcity of primary prey (aphid), ladybirds consume and reproduce on conspecific/heterospecific eggs as alternative diets.

Keywords: Aphidophagy, egg consumption, ladybirds, oophagy.

THE egg, which is the first life stage of many animal groups is immobile and prone to immense predation risk. Consumption of eggs as a source of nutrition is pronounced from primitive to advanced animal groups like insects[1], molluscs[2], fishes[3], amphibians[4], reptiles[5], birds[6] and mammals[7], as they are an easy meal with good nutritional profile[8]. The consumption of eggs or oophagy has been broadly classified as obligate[2] and facultative oophagy[3].

The eggs that are consumed can be either conspecific or heterospecific, with the former known as cannibalism. While cannibalism per se is known to be enhanced under food scarcity[9] and is considered beneficial to some extent[10], the reasons behind the evolution of heterospecific oophagy are not fully understood[2,5].

From an adaptive perspective, eggs serve as a source of food during egg-laying, mating and emigration[11]. Egg consumption largely depends on the associated benefits and costs. It may occur due to any of the following reasons: (i) to obtain proteinaceous diet, energy and nutrients; (ii) to remove any immediate potential competitor or predator in the surrounding for food, physical resources (e.g. egg-laying sites), and/or shelters; (iii) to get reproductive gain by reducing the fitness of other individuals of the same sex, and (iv) to enhance direct benefits for the related individuals in terms of survival and reproduction by eliminating genetically unrelated individuals[12,13]. However, the major disadvantages of egg consumption are: (i) risk of injury, (ii) disease or parasite transmission, and (iii) reduction in inclusive fitness by consuming relatives[14]. Thus, egg consumption may affect the distribution and abundance of species within agroecosystems.

Aphidophagous ladybirds rely mainly on aphids as their prime source of food[15], and due to ephemeral aphid colony they have to face severe risk of food scarcity[16]. Thus, cannibalism and intraguild predation (IGP) are alternative tactics for the sustenance of life in low food environment[17]. The consumption of conspecific life stages, viz. eggs[18], larvae[17] and pupae[19] comes under cannibalism whereas in IGP, susceptible heterospecific life stages of guild members are consumed[20]. Both phenomenon govern the structure of population and community by utilization of available resources at the site of feeding and reduction of competitors[16,21]. In ladybirds, post-hatching neonates consume eggs as their first meal because of limited foraging or searching capacity[22], poor predatory ability[23] and restricted walking speed[24]. The cannibalistic behaviour of ladybirds is a major concern in their mass production for biological control[25]. However, the importance of first meal for survival has been studied in ladybirds[26].

Among the two sexes, propensity of egg cannibalism is usually varied and more pronounced after mating. Recently, a study on *Coleomegilla maculata* (Degeer) demonstrated that the females cannibalized more eggs after mating; however, the opposite was observed for males[27]. It was also observed that females of herbivorous ladybird, *Henosepilachna pustulosa* (Kono) consume eggs because they provide a resource that helps the former in their own egg production[28].

The present study aims to evaluate the consumption rate of ladybird *Menochilus sexmaculatus* (Fabricius), on different diets and may provide information about resource allocation to various life attributes of ladybirds, and how egg consumption affects mating and reproductive parameters. The objectives of this study were to find answers to the following questions: (i) What would be the number of conspecific and heterospecific eggs consumed? (ii) Will the ladybird be able to complete development on conspecific and heterospecific egg diet? (iii) What kind of diet (aphids, conspecific eggs and heterospecific eggs) is the best in terms of development and reproduction?

We hypothesized that due to the presence of defensive surface chemicals on eggs of other species[29], the predatory stages of ladybirds will prefer more conspecific eggs. Moreover, apart from aphids being their natural diet, the performance of ladybirds in terms of development and reproduction would be better on conspecific eggs due to their nutritive value and known surface chemical compared to heterospecific eggs. Though the effect of egg consumption on predatory performance and developmental attributes has been evaluated earlier, that on reproduction is largely neglected. This study is likely to help us comprehend the cannibalism and IGP, and the conditions that induce egg consumption for sustenance of life.

Adults of *M. sexmaculatus* (*n* = 50) and *Propylea dissecta* (Mulsant; *n* = 50) were collected from agricultural fields of Lucknow, Uttar Pradesh, India (26°50′N, 80°54′E). They were brought to the laboratory and paired in transparent plastic Petri dishes (9.0 × 2.0 cm) and provided with *ad libitum* bean aphid, *Aphis craccivora* Koch, on their host plant, *Vigna unguiculata* L. (reared in a polyhouse at 25° ± 2°C; 65 ± 5% relative humidity (RH); 14 h light: 10 h dark photoperiod). The mating pairs of both species were kept under standard laboratory conditions (27° ± 2°C; 65% ± 5% RH; 14 h light: 10 h dark photoperiod) in a BOD incubator (Yorco; York Scientific Industries Pvt Ltd, Ghaziabad) for egg-laying. Daily fresh aphids were provided on their host plant *V. unguiculata* (taken from the polyhouse maintained at the aforesaid standard conditions). After every 24 h, eggs laid were separated and incubated under the above abiotic conditions until hatching. Newly hatched larvae of both species were reared separately in plastic beakers (14.5 × 10.5 cm; five larvae per beaker, covered with a muslin cloth to prevent escape of larvae) until they reached the third instar larval stage, after which they were isolated in Petri dishes (size as above) and reared till adult emergence. The experimental stages were taken from the stock population.

Ten-day-old well-fed males and females of *M. sexmaculatus* ($n = 50$) and *P. dissecta* ($n = 50$) were taken from the laboratory stock. They were paired in the transparent Petri dish (9.0 × 2.0 cm) and allowed to mate. After completion of mating, females of both species were isolated and kept individually in the Petri dish (size as above) with *ad libitum* supply of bean aphid, *A. craccivora* (taken from the polyhouse maintained at the above-mentioned conditions) under standard laboratory conditions (as above) in the BOD incubator for egg laying. At every 24 h, replenishment of aphids was done. Eggs were collected daily and used as diet for further experiments.

Prior to the start of the actual experiment, the number of eggs required by each larval stage to develop into successive larval stage was standardized. Fifty conspecific and heterospecific eggs (of *P. dissecta*) were given to the first, second, third and fourth larval instars of *M. sexmaculatus*. After every 24 h, the remaining eggs were counted. Different number of conspecific and heterospecific eggs were not consumed by the first (37.00 ± 3.00 and 40.00 ± 2.00 eggs respectively), second (36.00 ± 2.00; and 39.00 ± 2.00 eggs respectively) and third instars (29.00 ± 4.00 and 32.00 ± 2.00 eggs respectively) in 24 h, when provided with 50 eggs. However, the fourth instar larvae consumed all 50 eggs in 24 h. From this observation, we inferred that the fourth instar could consume more than 50 eggs. Thus, we decided to double the number of eggs (conspecific and heterospecific) given to them. After 24 h, 20.00 ± 17.00 conspecific and 35.00 ± 5.00 heterospecific eggs were left, and 100 eggs were found to be sufficient for the fourth instar to enter into pupation. The same number (100 eggs) was found sufficient for adults too (Figure 1). The ones that were not consumed were found to hatch.

Neonates of *M. sexmaculatus* ($n = 300$) were taken from the stock and placed individually in Petri dishes (9.0 × 2.0 cm) under standard abiotic conditions (27 ± 2°C; 65% ± 5% RH; 14 h light: 10 h dark photoperiod) in the BOD incubator. They were divided equally ($n = 100$) and placed in any one of the three groups having the following diet: (i) *ad libitum* (50 mg) supply of *A. craccivora*, (ii) *ad libitum* (100 eggs to maintain consistency for all the instars and adults) supply of conspecific eggs, and (iii) *ad libitum* (100 eggs due to the above reason) supply of hetero-specific eggs (of *P. dissecta*). These diets were replenished every 24 h till adult emergence. Duration of different instars, pre-pupal and pupal periods was recorded on each diet. The survival of offspring was recorded after pupal eclosion. The body mass of the newly emerged adults (from each diet) was also recorded using an electronic balance (Sartorius CP225-D, Germany; 0.01 mg precision).

Fifty newly emerged adults were taken from each of the groups. They were reared individually in Petri dishes (size as mentioned above) under standard abiotic conditions in the BOD incubator. They were provided with similar diet as received during immature stage development, which was replenished after every 24 h. At 10 days of age, 10 pairs were formed per group and allowed to mate once. The mating parameters, viz. time of commencement of mating (TCM) and copulation duration (CD) were recorded. Post-mating, the mated females from each group were isolated and kept individually in new Petri dishes (size as above) with *ad libitum* supply of the same diet. The latency to oviposit (LTO; time taken by mated females for first egg-laying) was recorded. Eggs laid were separated every 24 h and females were transferred to new and clean Petri dishes (size as above) with fresh diet. The daily oviposition and per cent egg viability were recorded for the next seven consecutive days.

The data were subjected to Kolmogorov–Smirnov test of normality and Bartlett's test of homogeneity of variance. They were found to be normally distributed with equal variance.

Data on developmental duration of all the immature stages and total developmental period (TDP), and body mass of newly emerged adults were subjected to one-way ANOVA, with diet (aphids, conspecific eggs and heterospecific eggs) as an independent factor. Egg consumption was subjected to two-way ANOVA with diet and life stage as independent factors. Comparisons between means

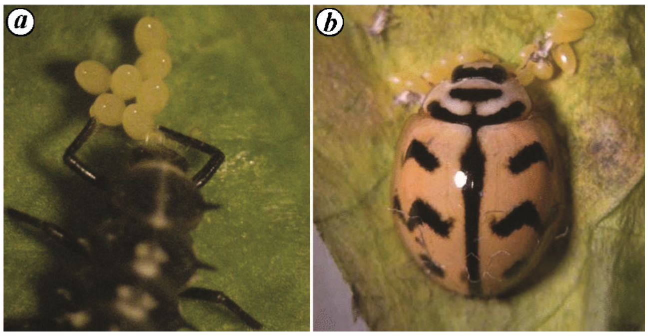

Figure 1. The life stages: (***a***) larva and (***b***) adult *Menochilus sexmaculatus* preying on eggs.

Table 1. Developmental duration of immature life stages of *Menochilus sexmaculatus* at aphids, conspecific eggs and heterospecific eggs

	Developmental duration (days)		
Immature life stages	On aphids	On conspecific eggs	On heterospecific eggs
First instar (L1)	1.19 ± 0.04^{aB}	2.44 ± 0.05^{bB}	3.38 ± 0.06^{cC}
Second instar (L2)	1.21 ± 0.04^{aB}	2.42 ± 0.06^{bB}	3.36 ± 0.06^{cC}
Third instar (L3)	1.24 ± 0.04^{aB}	2.71 ± 0.06^{bC}	3.18 ± 0.07^{cB}
Fourth instar (L4)	2.49 ± 0.07^{aD}	3.66 ± 0.05^{bE}	4.05 ± 0.08^{cE}
Prepupa	0.76 ± 0.03^{aA}	1.12 ± 0.03^{bA}	1.13 ± 0.04^{bA}
Pupa	2.01 ± 0.04^{aC}	3.09 ± 0.06^{bD}	3.59 ± 0.08^{cD}
Total developmental duration	8.92 ± 0.12^{aE}	15.40 ± 0.14^{bF}	18.48 ± 0.14^{cF}

Values are mean ± SE. Small letters as superscript denote the comparison of means between different types of diets. Capital letters as superscript denote comparison of means between different immature stages. Similar letters indicate lack of significant difference at $P > 0.05$.

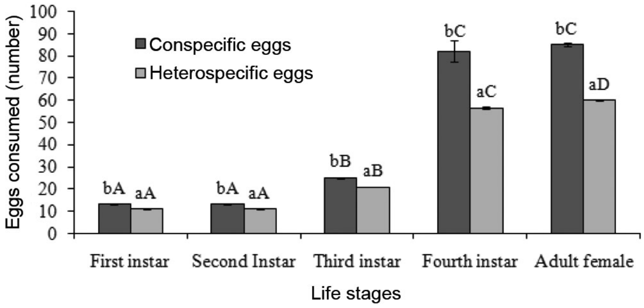

Figure 2. Number of conspecific eggs and heterospecific eggs consumed by different life stages of *M. sexmaculatus*. Values are mean ± SE. Small letters represent comparison of means between eggs consumed by a life stage. Capital letters represent comparison of means between life stages. Similar letters indicate lack of significant difference at $P > 0.05$.

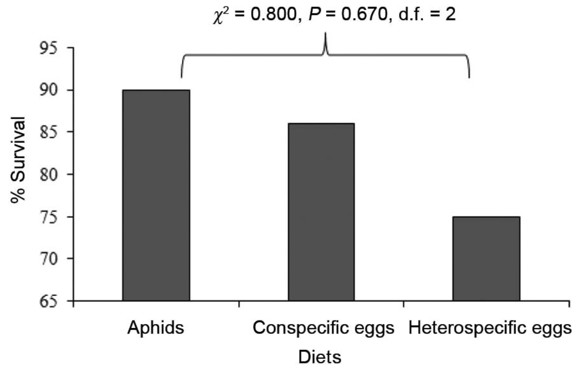

Figure 3. Percentage survival of *M. sexmaculatus* offspring under different diets (aphids, conspecific eggs and heterospecific eggs).

were made by post-hoc Tukey's honest significant difference test at 5% levels. Percentage survival of offspring post eclosion was subjected to chi square analysis.

TCM, CD and LTO were subjected to one-way ANOVA with diet as an independent factor. Daily oviposition and per cent egg viability were subjected to two-way ANOVA with diet and day of oviposition acting as independent factors. Comparisons between means were made by post-hoc Tukey's honest significant difference test at 5% levels. All statistical analyses were performed using MINITAB (2016).

Conspecific eggs were consumed in significantly higher number than heterospecific ones. There was significant interaction of egg diet (conspecific and heterospecific eggs) and life stage ($F = 621.11$, $P < 0.0001$, df = 4, 749) on egg consumption. Fourth instar and adult females consumed more number of conspecific and heterospecific eggs than other stages (Figure 2).

One-way ANOVA also revealed a significant effect of different diets (aphids, conspecific eggs and heterospecific eggs) on developmental duration of first ($F = 482.94$, $P < 0.0001$, df = 2, 284), second ($F = 392.25$, $P < 0.0001$, df = 2, 264), third ($F = 327.76$, $P < 0.0001$, df = 2, 257) and fourth ($F = 155.50$, $P < 0.0001$, df = 2, 251) instars, pre-pupal ($F = 40.89$, $P < 0.0001$, df = 2, 250), pupal ($F = 176.64$, $P < 0.0001$, df = 2, 250) and total developmental period ($F = 1307.42$, $P < 0.0001$, df = 2, 250). The developmental duration of the four larval instars, prepupa and pupa was shortest on aphid diet, followed by conspecific eggs, and longest on heterospecific eggs (Table 1).

Chi-square goodness-of-fit test revealed insignificant effects of different diets on percentage of survival ($\chi^2 = 0.800$, $P = 0.670$, df = 2), although maximum survival (90%) was recorded on aphid diet and lowest (75%) on heterospecific egg diet (Figure 3).

The results of one-way ANOVA demonstrated significant effect of different diets on body mass of the newly emerged adults ($F = 36.54$, $P < 0.0001$, df = 2, 250). Maximum body biomass of adults was found when immature life stages were fed on aphid diet, while minimum body biomass was observed when fed on heterospecific eggs (Table 2).

One-way ANOVA revealed significant effect of different diets on the time of commencement of mating ($F = 18.23$, $P < 0.0001$, df = 2, 29) and copulation duration ($F = 18.47$, $P < 0.0001$, df = 2, 29). Ladybirds reared

Table 2. Body mass of newly emerged adults, time of commencement of mating, copulation duration and latency to oviposit of *M. sexmaculatus* on three different diets: aphids, conspecific eggs and heterospecific eggs

	Diets		
Parameters	Aphids	Conspecific eggs	Heterospecific eggs
Body mass of newly emerged adults (mg)	11.18^b	9.02^a	8.50^a
Time of commencement of mating (min)	2.13^a	2.90^b	3.14^b
Copulation duration (min)	171.00^c	160.90^b	135.00^a
Latency to oviposit (days)	1.10^a	2.20^b	2.30^b

Values are mean ± SE. Small letters as superscript denote comparison of means. Similar letters indicate lack of significant difference at $P > 0.05$.

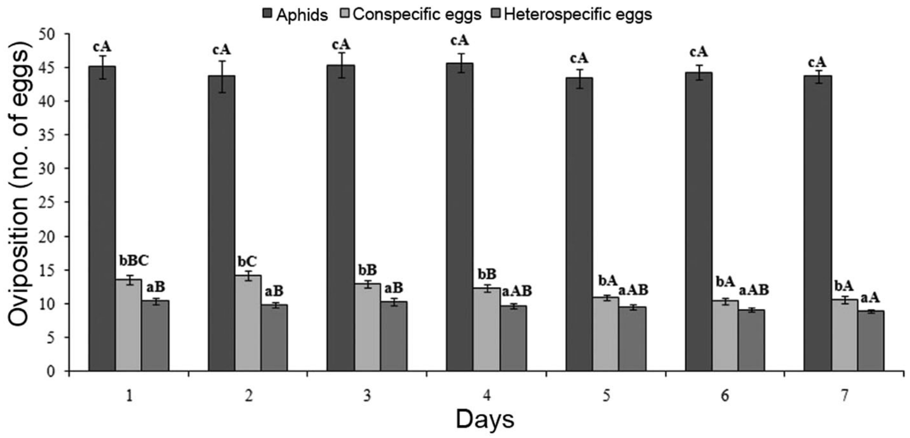

Figure 4. Daily oviposition by *M. sexmaculatus* on aphids, conspecific eggs and heterospecific eggs. Values are mean ± SE. Small letters represent comparison of means between aphids, conspecific eggs and heterospecific eggs. Capital letters represent comparison of means between days. Similar letters indicate lack of significant difference at $P > 0.05$.

on aphids took less time to commence mating compared to those reared on conspecific and heterospecific eggs. Similarly, copulation duration of ladybirds reared on aphids was longest, while those reared on heterospecific eggs copulated for the shortest duration (Table 2). One-way ANOVA showed significant effect of different diets on latency to oviposit ($F = 26.02$, $P < 0.0001$, $df = 2, 29$). Females reared on aphid diet took minimum time to lay their first egg batch, followed by conspecific and heterospecific egg diets (Table 2).

The results of two-way ANOVA also revealed significant effect of different diets ($F = 2638.51$, $P < 0.0001$, $df = 2, 209$) and days of oviposition ($F = 2.17$, $P < 0.05$, $df = 6, 209$) on daily oviposition. However, the interaction between diets and days of oviposition insignificantly influenced oviposition ($F = 0.66$, $P = 0.791$, $df = 12, 209$). Females laid more number of eggs on aphid diet followed by conspecific and heterospecific egg diet on each day (Figure 4). Similarly, there was significant effect of different diets ($F = 63.75$, $P < 0.0001$, $df = 2, 209$) on per cent egg viability. However, the days of oviposition ($F = 1.49$, $P = 0.183$, $df = 6, 209$) and the interaction between different diets and days of oviposition ($F = 1.21$, $P = 0.282$, $df = 12, 209$) insignificantly influenced per cent egg viability. In contrast, the per cent viability of eggs from different days of oviposition was highest on heterospecific diet compared to conspecific egg and aphid diets (Figure 5).

The study reveals that all ladybird stages consume more conspecific eggs than heterospecific eggs. The alkanes present on the egg surface and alkaloids present in the haemolymph are rich in defensive infochemicals/semiochemicals, which probably decrease the palatability of heterospecific eggs[29]. These alkanes and alkaloids have been previously reported to play a major role in attracting conspecific stages[16], and repelling or defending against heterospecifics[30]. In ladybirds, consumption of heterospecific eggs may cause the attacker to suffer due to ingestion of toxicants, or unpalatable or incompatible chemicals[29]. Detrimental effects on life-history traits and predatory performance in ladybirds have been also reported on consumption of intraguild prey[31].

Immature life stages of *M. sexmaculatus* developed fastest on aphid diet followed by conspecific egg diet compared to heterospecific eggs. Similarly, a study on the developmental duration of fourth instar larvae of *Coccinella septempunctata*, advocated that it was longer on conspecific egg diet compared to aphids[26]. Size differences in adults were also evident with those reared on aphids being larger than the ones on egg diet. These findings are consistent with those of earlier studies that demonstrated high palatability of aphids over ladybird

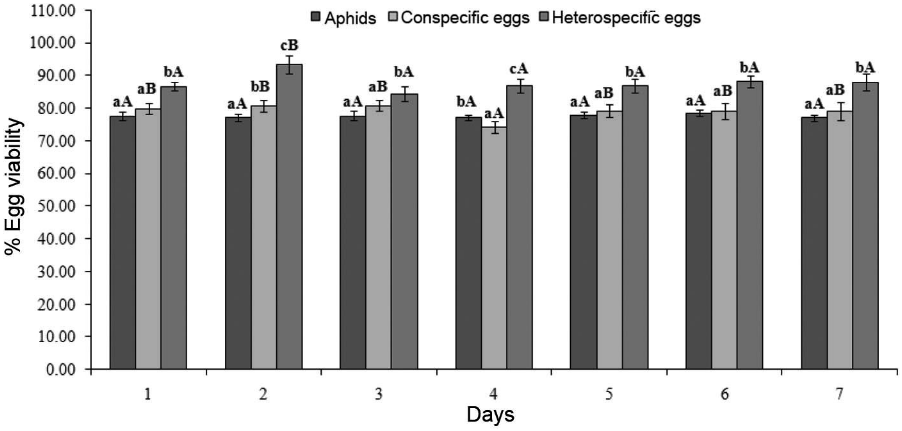

Figure 5. Daily per cent egg viability by *M. sexmaculatus* on aphids, conspecific eggs and heterospecific eggs. Values are mean ± SE. Small letters represent comparison of means between aphids, conspecific eggs and heterospecific eggs. Capital letters represent comparison of means between days. Similar letters indicate lack of significant difference at $P > 0.05$.

eggs[32]. The high nutritive value of aphids and their better utilization could be the most likely reason for fastest development and bigger size on aphid diet. The results are in accordance with earlier studies on ladybirds[33,34].

Lesser time to commence mating and longer copulation duration in aphid-fed adults compared to those fed on conspecific and heterospecific eggs may be attributed to the higher gain of energy and nutrients through aphid consumption. The highest consumption rate, conversion efficiency and growth have been reported on aphids than conspecific and heterospecific eggs in ladybird beetles, *C. septempunctata* and *Coccinella transversalis*[34]. For successful oviposition, aphidophagous ladybirds require the most suitable and essential prey, i.e. aphids[21]. Also, the time for latency to oviposition was less when fed on aphids, as it may cause early oogenesis due to fulfilment of necessary nutritional requirements.

The increased latency to oviposit on conspecific and heterospecific eggs vis-à-vis aphids, could also indicate the poor nutritional composition of these diets. Lesser oviposition on conspecific and heterospecific egg diets further supports the above. However, there was no termination of oviposition on egg diets. In adverse conditions like food scarcity, females also prefer less suitable hosts for oviposition[35]. Conspecific eggs are presumed to be a source of energy for both larvae and adults. Two-spot ladybird beetle, *Adalia bipunctata* is also known to consume and lay eggs on conspecific egg diet[36].

Per cent egg viability, however, followed a reverse trend with higher value for eggs of those females that were fed with conspecific and heterospecific egg diets. This can be attributed to the lack of hatching asynchrony. The hatching in small egg batches is generally synchronous, as observed during the experiment. This minimizes the chances of sibling egg cannibalism by neonates. When females lay more eggs in different batches on aphid diet, the chance of cannibalism or egg consumption by neonates increases due to higher hatching asynchrony[37,38]. This phenomenon is probably the reason for low per cent egg viability on aphid diet in the present experiment. The higher cannibalism or egg consumption probably causes significant egg mortality in coccinellids[39].

The overall biological and physiological performance was found to be poor for heterospecific egg diet. Moreover, the insignificant effect of diet on per cent survival suggests that immature life stages of *M. sexmaculatus* can also survive on eggs. Thus, the present study reveals that: (i) the developmental duration and reproductive parameters of ladybirds are modulated according to the type of diet they consumed; (ii) aphids are the best diet; (iii) larval stages and adults prefer more conspecific eggs as a food over heterospecific eggs, probably owing to low toxicity, and (iv) aphidophagous ladybirds can predate on conspecific/heterospecific eggs for sustenance, but with altered fitness.

In general, coccinellids are important agents of IGP. Therefore, their role in the removal of a particular pest needs to be considered in the broader context of the entire guild of natural enemies contributing to pest mortality. For example, this study implies that the aphidophagous species are not suitable for foreign introduction, even though they may be important biological control agents in their native ecosystems. Once established, they can simply replace aphid mortalities provided by local species, have non-target effects on other herbivores or even replace native species. Thus, future seems clear for improving the conservation and efficiency of naturally occurring species in open systems.

Conflict of interest: The authors declare no conflict of interest.

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