Difference in container size limits foraging and affects demographic attributes of ladybird beetle, *Menochilus sexmaculatus*

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The present study analyses the influence of container size available during foraging on the demographic attributes of ladybird beetle *Menochilus sexmaculatus* (Fabricius; Coleoptera: Coccinellidae). To provide variations in the foraging arena, we used a small petri dish, large petri dish, and beaker as small, medium and large containers for foraging. Results revealed significant influence of container size on life attributes. Developmental attributes of *M. sexmaculatus* were better in the small arena followed by medium and large arenas. The highest mortality rate and maximum life expectancy were recorded in a large arena, followed by medium and small arenas. Reproductive attributes (fecundity and oviposition period) were much better in the large arena. The results of this study indicate that a small container encompassing small foraging arena is beneficial for immature development and survival, while a large container encompassing large foraging arena is best for the reproductive attributes of adults.

Keywords: Development, life table, *Menochilus sexmaculatus*, prey searching, rearing container, reproduction.

LADYBIRD beetles are the most studied and successful insect predators of aphids[1]. The major environmental conditions which have an impact on establishing the population of ladybird beetles in the field include temperature, food availability, light–dark cycle and humidity[2]. Apart from these environmental conditions, preference–performance[3,4], guild formation, crowding, prey–predator ratio, larval cage and mating enclosures are well-known regulators of growth, development and survival of the developing instars[5]. Besides these, the rearing arena or container size is an important parameter to be taken into account while rearing larval instars.

Predator–prey interaction is a link to understand the behaviour and physiology of the foraging insect encountering its prey. Availability, density and distribution of prey are some of the key factors that determine the fitness of a predator sharing the same niche or area. Small arena with low prey density allows the predator to feed on all the prey available; but if this low density is probably not sufficient to fulfil its appetite, the predator will suffer from starvation. This is a condition that directly impacts the utilization and depletion of food reserves in the body of the insect. It results in lower level of energy contents stored in the body, thus affecting its fitness[6]. However, a small arena with high prey density minimize the energy lost during foraging and provide better chances for growth and development.

Opportunities received by a predator in a large arena with low prey density were the same as those in the small arena with low prey density. However, foraging in the large arena becomes much intensified as the predator has to cover a large area and spend much more energy in foraging, which ultimately allows insects to feed less prey. In this way, it receives a small amount of prey available which is not sufficient to satisfy its need. However, in a large arena with high prey density, incidences of prey encounters are more and energy expenditure during foraging is reduced.

To overcome aphids in the field, deliberate abundance of ladybird beetles in the affected area is essential. However, the question arises as to how one should correlate or synchronize the prey–predator ratio in a given area within a given unit of time. If the number of predators in the field is low and is not sufficient to control the very large number of available prey population, it would cause noticeable loss in the yield. To prevent this, one should focus upon the establishment of aphids followed by their biocontrol agent, i.e. ladybird beetles. It is a well-known fact that once these beetles are released in the field, they can establish their populations naturally, but if infestation of the pest is much higher, there is a need to release a few more beetles of some species. This can be achieved only by rearing and mass multiplying them in controlled environmental conditions on a natural or semi-natural diet[7]. Integrated pest management has emphasized the utilization of several coccinellid species against a large variety of aphids. This has caused increased demand

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of the biological agents, which can be fulfiled only by mass rearing them under controlled laboratory conditions.

Therefore the present study aimed to evaluate the influence of foraging arena on growth, development, survival and reproductive attributes of ladybird beetle *Menochilus sexmaculatus* (Fabricius; Coleoptera: Coccinellidae). The study will help determine which arena is better for growth of the larvae and reproduction of adults; and how the multiplication rate of immature stages and oviposition by adults can be maximized so that they can be used as an efficient biocontrol agent in the field within a short period of time.

Material and methods

For providing variation in foraging arena, we used a small-sized petri dish (95.46 cm^3), large-sized petri dish (441.96 cm^3) and beaker (603.43 cm^3) as small, medium and large foraging arena respectively.

Stock maintenance

The initial stock was cultured using adults of *M. sexmaculatus* collected from adjoining fields by the side of River Gomti in Lucknow district, Uttar Pradesh, India. They were allowed to mate; the mating pairs formed were transferred and kept in small-sized petri dishes. They were provided with aphid *Aphis craccivora* Koch (Hemiptera: Aphididae) obtained from *Dolichos lablab* Linnaeus (Fabales: Fabaceae). All the mating pairs kept in petri dishes were transferred in a biological test chamber (BTC) at 27° ± 2°C; 65 ± 5% relative humidity and 14:10 h light : dark photoperiod. The aphid supply was refreshed every 24 h. Adults were observed for their egg-laying twice a day. After oviposition, they were transferred to another petri dish and eggs laid were monitored for hatching. Larvae hatched from eggs were transferred into separate petri dishes using a fine brush. They were provided with *A. craccivora*. The complete set-up was monitored until adult emergence under controlled laboratory conditions. Separate stock cultures using large-sized petri dish and beaker were also maintained following the above procedure. Separate life stages were selected for separate experimental set-up.

Experimental design

Developmental attributes: Adults that emerged from the first generation of stock culture were transferred in petri dishes provided with *A. craccivora* and kept under controlled laboratory conditions until sexual maturity. Food supply was refreshed every 24 h. On attaining sexual maturity, mating pairs were isolated and transferred into petri dishes. Eggs laid by these mating pairs were collected and observed for hatching. After hatching, 50 first instar larvae were placed in 50 different petri dishes (size 9.0 × 1.5 cm) individually and were provided with *A. craccivora.* These were reared and monitored until adult emergence. The total number of larvae surviving in each instar was recorded. The duration of each immature stage and total developmental period were recorded. Adults were weighed within 24 h after their emergence. Pupation (number of pupae/number of first instars × 100), immature survival (number of adults emerged/number of first instars × 100), development rate (1/total development period) and growth index (percent pupation/mean larval duration) were estimated. The whole procedure was also repeated in large-sized petri dishes (size 15 × 2.5 cm) and beakers (size 12 × 8 cm).

Data in per cent values were transformed using arcsine square root transformation prior to analysis. The results were analysed using one-way ANOVA and means were compared using Tukey's test ($\alpha = 0.05$) and statistical software MINITAB on a personal computer. Pearson's correlation analysis was used to assess influence of development rate on weight of adults. Analysis of covariance (ANCOVA) was used to assess the development rate influenced indirectly by weight used as the covariate.

Mortality life table parameters: Age and stage-specific mortality life table parameters were calculated following Morris and Miller[8].

Life expectancy (ex): This is the average life remaining for individuals of a particular stage (x) and is calculated as

$$ex = T_x/L_x,$$

where L_x is the average number of alive during any particular stage, and T_x is the total number of individuals of stage unit beyond stage x.

Mortality-survivor ratio (MSR): This shows the ratio between dead and alive individuals in a specific life stage (x) was not found.

$$MSR = \frac{\text{Mortality in the specific stage}}{L_x \text{ of subsequent stage}}.$$

Indispensable mortality (IM): Presumable mortality that have not occurred if the factor causing it was absent

$$IM = \text{Total number of adults} \times MSR \text{ of the stage}.$$

Reproductive attributes: To evaluate the reproductive performance of *M. sexmaculatus*, adults that emerged

Table 1. Developmental duration (days; mean ± SE) of larval stages of *Menochilus sexmaculatus* ($n = 50$ per treatment) reared in different foraging arenas (d$f = 2, 117$). Means within rows with the same letter are not significantly different ($\alpha > 0.05$)

Stage	Foraging arena			*F*-value	*P*-value
	Small arena	Medium arena	Large arena		
Incubation period	2.45 ± 0.11a	2.50 ± 0.11a	2.70 ± 0.11a	1.41	0.253
First instar	1.45 ± 0.11a	1.70 ± 0.11a	2.10 ± 0.07b	11.19	<0.001
Second instar	1.65 ± 0.11a	2.15 ± 0.08b	2.60 ± 0.11c	21.63	<0.001
Third instar	2.10 ± 0.07a	2.60 ± 0.11b	3.20 ± 0.09c	35.29	<0.001
Fourth instar	2.40 ± 0.11a	3.35 ± 0.11b	3.80 ± 0.09c	46.40	<0.001
Pre-pupa	1.10 ± 0.07a	1.85 ± 0.08b	2.15 ± 0.08c	48.33	<0.001
Pupa	2.65 ± 0.11a	3.70 ± 0.11b	4.80 ± 0.09c	110.26	<0.001
Total larval period	7.60 ± 0.17a	9.80 ± 0.22b	11.70 ± 0.18c	113.73	<0.001
Total pupal period	3.75 ± 0.14a	5.55 ± 0.14b	6.95 ± 0.14c	135.50	<0.001
Total developmental period	13.80 ± 0.24a	17.85 ± 0.30b	21.35 ± 0.28c	188.58	<0.001

from the experiment were paired and kept in small petri dishes (9.0 × 1.5 cm) for lifetime under controlled laboratory conditions. These pairs ($n = 10$) were allowed to feed on *A. craccivora* infested on host plant leaves. The aphids and leaves were replaced with fresh ones every 24 h. Daily oviposition and their viability were recorded for lifetime. The experiment was replicated ten times with the pair in the petri dish considered as a replicate. The whole procedure was also replicated in large-size petri dishes (15 × 2.5 cm) and beakers (12 × 8 cm).

The pre-oviposition period (from adult emergence until first oviposition), oviposition period (from first to last day of oviposition) and post-oviposition period (from last oviposition until death) were recorded. Per cent egg viability (number of eggs hatched/number of eggs laid × 100), reproductive rate (fecundity/oviposition period) and reproductive time ratio (reproductive period/non-reproductive period) were calculated from the data obtained. The non-reproductive period was the sum of pre- and post-oviposition periods.

The results were analysed using one-way ANOVA and means were compared using Tukey's test ($\alpha = 0.05$) with statistical software MINITAB. Data on reproductive attributes, viz. female weight and fecundity, pre-oviposition, oviposition and post-oviposition periods, male weight and egg viability were subjected to regression analysis to obtain the best relationship.

Fertility life table: Data obtained on lifetime oviposition for each treatment were used for the calculation of fertility life table parameters following Lotka[9] and Birch[10].

Results

Developmental attributes

Results revealed significant difference among developmental durations of various life stages of *M. sexmaculatus* (Table 1). The incubation period was found to be shortest in the small arena followed by the medium and large arenas. However, the difference between individual means was not statistically significant. First instar larvae took the shortest time to molt into next instars when reared in the small arena, followed by medium and large arenas. Individual means were also significantly different. Developmental duration of second, third, fourth instars, pre-pupa and pupa was also found to be shortest when reared in the small arena followed by medium and large arenas. Individual means were also found to be significantly different for these immature stages. Total larval period, total pupal period and total developmental period were the shortest when reared in the small arena followed by medium and large arenas. Individual means were also significantly different for these parameters. Per cent pupation, per cent adult emergence and growth index were found to be better for the small arena (93.33%, 93.33%, 12.28 respectively) followed by medium (76.67%, 76.67%, 7.82 respectively) and large (70.00%, 66.67%, 5.98 respectively) arenas. The development rate was higher in the small arena (0.07) followed by medium (0.06) and large (0.05) arenas. Overall mortality was greater in the large arena (20.00%) followed by medium (12.00%) and small (8.00%) arenas. The survival of each immature stage was highest when reared in the small arena and lowest when reared in the large arena (Table 2). Weight of females was found to be 13.23 ± 0.17, 11.10 ± 0.08 and 8.98 ± 0.08 g for small, medium and large arena respectively. Weight of male was 11.32 ± 0.15, 10.07 ± 0.07 and 6.26 ± 0.06 mg for small, medium and large arena respectively. Weight of adults was positively correlated with foraging arena ($r = 0.768$, $P < 0.001$). Analysis of covariance showed that the foraging arena ($F = 29.58$, $P < 0.001$, d$f = 2, 147$) had a significant effect on development rate in comparison to weight of adults ($F = 0.52$, $F = 0.477$, d$f = 1, 147$).

Mortality life table

Age-specific life table: Age-specific survival of immature stages of *M. sexmaculatus* was highest and apparent

Table 2. Stage-specific life table of larval stages of *M. sexmaculatus* reared in different foraging arenas

	Age (X)	Age-specific survival (l_x)	Number dying (d_x)	Apparent mortality (100 q_x)	Real mortality (100 r_x)	Survival rate (S_x)	k-Value	Mortality survival ratio	Indispensable mortality
Small arena									
	First instar	50	1.00	2.00	1.00	0.98	0.01	0.02	0.38
	Second instar	49	2.00	4.08	2.00	0.96	0.02	0.04	0.78
	Third instar	47	1.00	2.13	1.00	0.98	0.01	0.02	0.40
	Fourth instar	46	0.00	0.00	0.00	1.00	0.00	0.00	0.00
	Pre-pupa	46	0.00	0.00	0.00	1.00	0.00	0.00	0.00
	Pupa	46	0.00	0.00	0.00	1.00	0.00	0.00	0.00
	Adult emergence	46				Kappa = 0.036			
Medium arena									
	First instar	50	2.00	4.00	2.00	0.96	0.02	0.04	0.68
	Second instar	48	1.00	2.08	1.00	0.98	0.01	0.02	0.35
	Third instar	47	1.00	2.13	1.00	0.98	0.01	0.02	0.36
	Fourth instar	46	0.00	0.00	0.00	1.00	0.00	0.00	0.00
	Pre-pupa	46	1.00	2.17	1.00	0.98	0.01	0.02	0.37
	Pupa	45	1.00	2.22	1.00	0.98	0.01	0.02	0.38
	Adult emergence	44				Kappa = 0.056			
Large arena									
	First instar	50	4.00	8.00	4.00	0.92	0.04	0.08	1.20
	Second instar	46	2.00	4.35	2.00	0.96	0.02	0.04	0.65
	Third instar	44	1.00	2.27	1.00	0.98	0.01	0.02	0.34
	Fourth instar	43	2.00	4.65	2.00	0.95	0.02	0.05	0.70
	Pre-pupa	41	1.00	2.44	1.00	0.98	0.01	0.02	0.37
	Pupa	40	0.00	0.00	0.00	1.00	0.00	0.00	0.00
	Adult emergence	40				Kappa = 0.097			

mortality was lowest when reared in the small arena, followed by medium and large arenas. Results revealed that as the larvae entered the next stage, their life expectancy decreased subsequently. Life expectancy was found to be lowest for the small arena, followed by medium and large arena (Figure 1).

Stage-specific life table: Stage-specific survival was highest for the small arena followed by medium and large arenas (Table 2). Apparent mortality and real mortality were lowest in the small arena, while they were highest in the large arena. MSR was lowest for all immature stages, except second instars in the small arena. IM was recorded only in early larval instars in the small arena. It was found to be maximum for first instars reared in the large arena. Overall Kappa value was lowest in the small arena followed by medium and large arenas.

Reproductive attributes

Pre-oviposition period, post-oviposition period, per cent egg viability and reproductive time ratio were not influenced by the foraging arena (Table 3). There was significant influence of different foraging arenas on the oviposition period, fecundity and reproductive rate, which were shortest in the small arena followed by medium and large arenas. Fecundity increased with increase in age up to a certain time; thereafter it gradually decreased (triangular fecundity function) in all three treatments (Figure 2). Regression analysis revealed that female weight positively correlated with oviposition period ($r^2 = 0.780$, $F = 68.24$, $P < 0.001$) and fecundity ($r^2 = 0.962$, $F = 200.54$, $P < 0.001$). However, female weight did not influence pre-oviposition period ($r^2 = 0.722$, $F = 1.85$, $P = 0.184$) and post-oviposition period ($r^2 = 0.536$, $F = 1.25$, $P = 0.273$). Male weight did not influence egg viability ($r^2 = 0.722$, $F = 1.85$, $P = 0.185$).

Fertility life table: Net reproductive rate and mean generation time were highest in the large arena followed by medium and large arenas (Table 4). Intrinsic and finite rate of increase were maximum in the small arena followed by medium and large arenas. Doubling time was maximum in the medium arena followed by large and small arenas.

Discussion

The present study reveals significant influence of foraging arena on the growth, development, survival and reproduction of *M. sexmaculatus*. A small arena encompasses limited space to forage food, as it is easily available in a confined arena. Thus, the larvae need not spend extra energy in search of prey compared to a medium or

large arena. Failure to balance daily energy expenditure with daily energy intake can seriously affect the survival of the predator[11]. Minimizing foraging intensity in a confined arena can minimize the rate of prey consumption. It might be possible that decrease in energy expenditure by the larvae results in a slow metabolic rate. From the experimental results, it can be mentioned that larvae reared in the small arena utilize maximum amount of energy for their growth and maintenance during, which in turn results in increased body mass of the adults. In a study using *Harmonia axyridis* reared under different sized containers, significant influence on fresh weight was reported[12]. A small arena enhances the limited movement not only for the predator, but also of the prey. Consequently, it will be much easier to chase and compete with the prey to feed upon by the predator. In this way, the developmental rate and growth index of larvae become much higher in the small arenas as compared to the other foraging arenas. In a study using *Aurelia aurita* as a predator of *Mallotus villosus*, a small-sized container was found to overestimate the rate of predation[13]. The foraging arena did not significantly influence incubation period of the eggs. This can be ascribed to the overall parental investment prior to the egg-laying[14], which must be unaffected by the foraging arena. All the eggs were collected from the young and freshly mated adult females which improved the quality and viability of the eggs, because delayed mating of adults can have a negative effect on reproductive attributes and result in more non-viable eggs laid by females[15].

Higher mortality in the beaker may be due to the greater space covered by the larvae in search of the food. Hence, it might be assumed that high prey searching rate may lower the vigour of the larvae. Besides, aphids also tend to move and cover a larger area. Although aphids were supplied to the larvae together with their host plant leaves, in a large arena most of the aphids were found to move around probably after being well-fed. When necessary they start to forage and approach the leaves. During this foraging, they lose most of their energy, which in turn makes them less nutritious for the predator larvae. Even though these aphids provide less nutrition to the predators, still the later have to spend the same amount of energy to consume the former. Thus, it is clear that within a given period of time larvae are feeding upon sufficient quantity of aphids, but not getting the requisite quality of aphids because predator foraging is limited by time, thus consequently lowering the capturing and feeding efficiency[16].

Several previous studies have reported that heavier females were more fecund in comparison to light-weight females[17,18]. Contradictory to these findings, the present study reveals that fecundity, oviposition period and oviposition rate are maximum in the case of light-weight females reared in beakers. This interesting finding might be a strategy of the female to utilize the aphids distributed in an enclosed arena. Immature stages and even the fourth instars are less active than the adult female and male. To cover a proper foraging arena, they creep continuously in order to fill their gut completely. This utilizes a large share of their energy reserves. On the other hand, adults move faster and cover that foraging area creeping and flying to capture their prey[19]. This can gradually

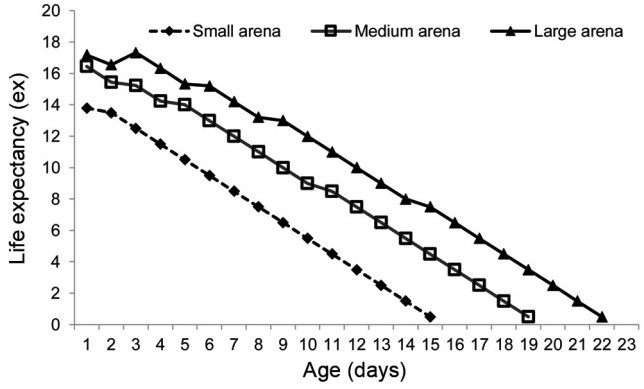

Figure 1. Age-specific life expectancy of immature stages of *Menochilus sexmaculatus* reared in different foraging arenas.

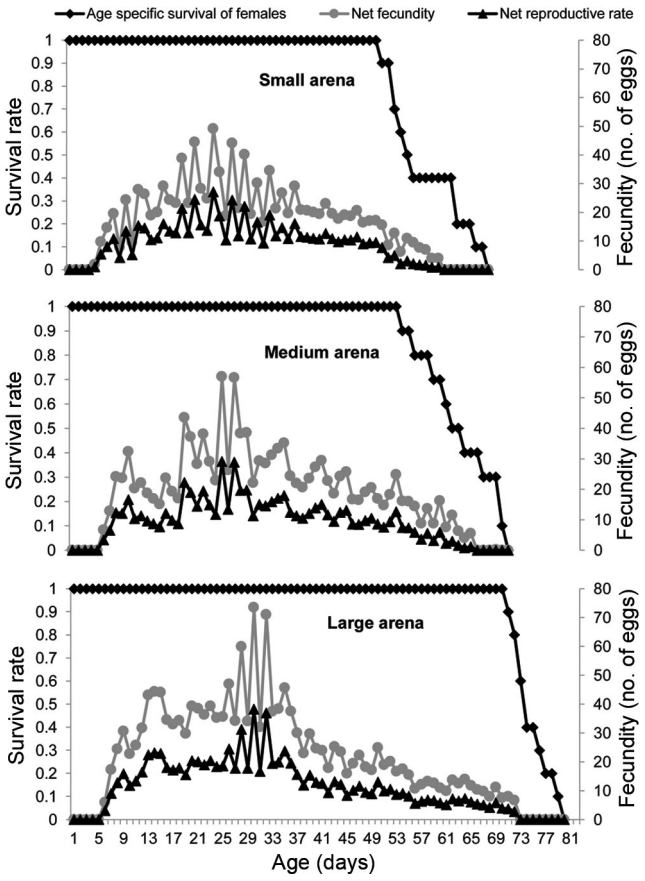

Figure 2. Demographic attributes of *M. sexmaculatus* reared in different foraging arenas.

Table 3. Reproductive attributes (mean ± SE) of *M. sexmaculatus* ($n = 10$ per treatment) reared in different foraging arenas (d$f = 2, 27$). Means within rows with the same letter are not significantly different ($\alpha > 0.05$)

Reproductive attributes	Foraging arena			*F*-value	*P*-value
	Small arena	Medium arena	Large arena		
Pre-oviposition period (days)	5.50 ± 0.31a	5.90 ± 0.23a	6.10 ± 0.23a	1.38	0.269
Oviposition period (days)	45.30 ± 1.76a	50.50 ± 1.85a	62.10 ± 0.74b	31.43	<0.001
Post-oviposition period (days)	5.30 ± 0.37a	5.10 ± 0.31a	5.70 ± 0.21a	1.00	0.380
Lifetime fecundity (eggs)	1074.00 ± 34.60a	1280.40 ± 20.26b	1699.30 ± 33.05c	112.78	<0.001
Egg viability (%)	90.47 ± 1.00a	89.88 ± 0.60a	91.75 ± 0.79a	0.29	0.753
Reproductive rate	23.83 ± 0.66a	25.70 ± 1.12a	27.37 ± 0.47b	37.98	<0.001
Reproductive time ratio	4.30 ± 0.30a	4.69 ± 0.31a	5.29 ± 0.13a	0.83	0.447

Table 4. Demographic parameters of *M. sexmaculatus* reared in different foraging arenas

Foraging arena	Net reproductive rate (R_o)	Intrinsic rate of increase (r_m)	Mean generation time (T_c)	Doubling time	Finite rate of increase (λ)
Small arena	619.72	0.22	28.89	2.19	1.25
Medium arena	677.32	0.21	31.17	2.26	1.23
Large arena	906.54	0.21	32.25	2.25	1.23

minimize the time and energy spent in foraging, feeding and filling the gut capacity. Besides, females during their immature developmental stages experience the consequences of foraging in the small arena. Thus they tend to reduce the number of eggs laid since the small arena cannot support several larvae hatched from a large number of eggs laid. This could result in crowding and competition for available food[20]. On the contrary, the chances of competition as a consequence of crowding are minimized in a large arena; thus here females are found to fecund more.

Conclusion

The present study postulates that variation in foraging arena does have a significant influence on the life attributes of *M. sexmaculatus.* Larger foraging arena may slow the rate and duration of growth and development of immature stages that may also result in higher mortality The small arena facilitates larvae to complete their development within a short period of time in comparison to medium and large foraging arenas. In contrast, large arena is most suitable for reproduction and oviposition. In a small arena, females constrict or lower their oviposition which can be maximized by allowing them to inhabit a large arena. These results will help in the mass multiplying of *M. sexmaculatus* given the fact that immature stages are better in small arenas and adults in large foraging arenas.

Competing interests: None to declare.

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