Optimal ovipositional behaviour of Parthenium beetle, *Zygogramma bicolorata* Pallister (Coleoptera: Chrysomelidae)

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Oviposition is considered as one of the most critical events in the life cycle of phytophagous insects. The preference for a specific site for egg-laying depends not only on food availability and the presence of conspecific tracks, but also on the taxes, colour and curve of the surface of the oviposition site. The ovipositional behaviour of *Zygogramma bicolorata* Pallister in terms of geo- and phototaxis, colour and texture of substrates was examined. Negatively geotactic substrates were preferred by the insect for oviposition. However, there was no apparent preference for positively or negatively phototactic substrates. Studies on combination of taxes served to reinforce the results of taxes studied singly that the negatively geotactic response was most prominent. Female *Z. bicolorta* preferred green and plastic over the other colours and textures tested.

Keywords: Colour, geotaxis, oviposition, phototaxis, texture, *Zygogramma bicolorata*.

OVIPOSITION behaviour comprises a series of behavioural and physiological actions that commence with the movement of the egg through the oviduct, and ends with egg-laying on a substrate that can support larval development. Specialized structures and behaviour of the female assist her in laying the mature eggs within a protected environment during oviposition. Oviposition site preference is an important aspect of the successful development and survival of offspring. Females lay eggs on plant species or plant parts where the chances of survival of the offspring are the highest[1]. The driving forces which influence the foraging ability and approval or denial are largely governed by the quality of nutrition, competition and co-occurrence of appropriate conditions that ensure success of the progenies. Determinants of oviposition preference by phytophagous insects include allelochemicals, quality and quantity of resources, plant morphology and natural enemies[2,3]. A question is posed[4]: 'Does mother know best'? To find out the answer, numerous studies have been conducted[5,6]. Traditional optimization theory of host selection implies that in phytophagous insects, the female selects its host that offers maximum health benefits to its progenies[7]. This is often found in many insects where the selection of food is made by the female[8]. However, a number of studies have reported a negative relationship between host preference by the adults and its effects on larval performance[9,10], which was moderately elucidated by hypotheses, which explain the significance of environmental aspects and selection forces additional to the nutrition[11]. Among adults, females tend to search for suitable sites for oviposition, whereas males tend to be more concerned with the search for a suitable mate rather than in foraging[12]. Therefore, foraging behaviour of the females is often equated with the search for oviposition sites.

Parents and especially females may use a variety of defensive strategies other than behaviour to protect their offspring from predation. A key component for understanding the population dynamics in phytophagous insects is the correlation between the preference for oviposition sites by the females and the performance of successive progenies[13]. The reproductive success of an organism residing in a habitat where quality of food is not constant mainly depends on site selection and timing of egg-laying by the females. Several features of an oviposition site can influence the fitness of parents directly or indirectly by having an impact on hatching, larval development and survival[14]. Females choose a suitable site for oviposition and lay their eggs. At this stage, female investment is considered to be complete and the offspring are left to develop on their own. Oviposition site selection may have a significant influence on spatial distribution of a species. It can also affect population dynamics[15] and the structure of the communities[16].

The preference for a specific site for egg-laying is not only dependent on food availability and the presence of conspecific tracks, but also on the taxes, colour and curve of the surface, physical structure and chemical composition of the oviposition site[2,17]. Cues include colour[18], chemical markers put on the eggs during or following oviposition[19], chemicals released by the egg itself[20], chemicals in larval frass[21] and larval secretion[22]. Several studies have been conducted to determine the orientation of oviposition sites and preference for colour and texture in insects[23–27]. However, there are only a few studies on the Parthenium beetle, *Zygogramma bicolorata*. Thus, the

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present study examines the less explored aspects of oviposition in this beetle.

Materials and methods

Maintenance of stock culture

Adults of *Z. bicolorata* were collected from areas of Lucknow University, Uttar Pradesh, India, and allowed to mate in plastic petri dishes (9.0 × 2.0 cm). The mated pairs were then kept under controlled environment (27° ± 2°C; 65% ± 5% relative humidity (RH); 14 : 10 L : D) in environmental test chambers. Fresh chopped leaves of *Parthenium hysterophorus* Linnaeus were provided as food and were replaced daily. Eggs laid by the females were collected daily and hatched larvae were reared in plastic petri dishes till pupation. For pupation, fourth stage larvae were shifted to beakers (loaded with damp sand). After the completion of pupation, adults which emerged from the sand were reared separately.

Experimental protocol

To study ovipositonal orientation in *Z. bicolorata*, three experimental set-ups were designed[28]: (i) Orientation towards photo- and geotaxis, both singly and in combination. (ii) Orientation towards colour of substrata. (iii) Orientation towards texture of substrata.

Orientation towards taxes of substrata: To study ovipositional pattern of *Z. bicolorata* in relation to photo- and geotaxis, eight treatments were designed. For this, ten-day-old pairs were kept in each of the set-ups with the host plant leaves (replaced daily with fresh ones). The ovipositional pattern was recorded for the next 30 days. Each experiment was conducted in ten replicates. The eight set-ups were designed following the method of Omkar and Mishra[28].

To study the geotactic preference four set-ups were designed, viz. *A*, *B*, *C* and *D*, while to study the effect of light on geotaxis four set-ups were designed, viz. *E*, *F*, *G* and *H*. These set-ups were also used to study the combinations of photo- and geotaxis. Oviposition in the area exposed to light was considered positively phototactic (P_P), while that in the dark was taken as negatively phototactic (P_N). Eggs laid up to a height of 2 cm from the base (arbitrary) were considered as positively geotactic (G_P), whereas oviposition above that area and on the lower surface of the leaves was considered as negatively geotactic (G_N). Eggs laid parallel to the base of the set-up were taken as 100% G_N, while those on the walls of the set-up were considered as semi-G_N. The taxes P_PG_P, P_PG_N, P_NG_P and P_NG_N were found in set-ups *E*, *F*, *G* and *H*. In each of these four set-ups, one of the combinations of taxes was absent. The taxes absent in subsets *E*, *F*, *G* and *H* were P_PG_P, P_PG_N, P_PG_P and P_NG_P respectively. Egg-laying were recorded on a daily basis.

Orientation towards colour of substrata: To evaluate the ovipositional preference for different coloured substrata, six glazed papers of different colours, viz. white, green, yellow, red, blue and black were glued to an area 60° on both the surface and wall of the petri dishes (21.0 × 3.0 cm). Ten-day-old adults were allowed to mate and thereafter females were left to oviposit (one female per petri dish). Oviposition by females on each substrate was recorded for 30 days. The experiment was conducted in ten replicates.

Orientation towards texture of substrata: To assess the ovipositional preference for different textures of substrata, six different substrates, viz. white filter paper (Whatman's No. 1), coarse cardboard (1 mm thick), glass (plain transparent glass of petri dish only), excised leaves of *P. hysterophorus*, muslin (white) and plastic were glued to an area equivalent to a 60° arc on the lid, bottom and walls of the petri dishes (21.0 × 3.0 cm). Ten-day-old adults were then allowed to mate and females were left to oviposit in the petri dish with *Parthenium* leaves which replaced twice a day to avoid drying and yellowing. Oviposition by females on each substrate was recorded for the next 30 days. The experiment was conducted in ten replicates.

Statistical analysis

All the data generated on oviposition by the females were subjected to normality test using the Kolmogorov–Smirnov test and Bartlett's test for homogeneity of variance, before one-way ANOVA. All statistical analyses were done using MINITAB.15.0. Differences between individual means were calculated using post hoc Tukey's honest significance test at 5% level.

Results

Orientation towards taxes of substrata

Among two geotactic substrata, more number of eggs was recorded on negatively geotactic substrata in all the set-ups (Figure 1 and Table 1). The differences in individual means were insignificant among the sets *A*, *B*, *C*, *D*, *E*, *G*, and *H*. Higher oviposition was recorded on substrata that were absolutely parallel to the base (100% G_N) (Figure 2 and Table 2). The females oviposited on both P_P and P_N substrata, but no significant preference was found for these taxes. When a combination of taxes was observed, more egg-laying was observed on substrates that were in combination with G_N (Tables 3 and 4). In set-up *E*, maximum proportion of eggs (0.38) was oviposited on P_PG_N. In set-up F, maximum proportion of eggs (0.36) was

Table 1. Oviposition at different taxes by *Zygogramma bicolorata*

	Sets							
Taxes	*A*	*B*	*C*	*D*	*E*	*F*	*G*	*H*
G_P	73.2 ± 4.17^{a}	79.2 ± 7.23^{a}	24.7 ± 1.77^{a}	25.00 ± 1.66^{a}	45.80 ± 2.22^{a}	134.40 ± 9.75^{b}	16.40 ± 2.05^{a}	71.60 ± 2.04^{a}
G_N	306.4 ± 5.33^{b}	306.4 ± 9.37^{b}	83.3 ± 4.29^{b}	71.1 ± 3.68^{b}	183.2 ± 4.86^{d}	92.9 ± 11.39^{c}	111.2 ± 9.57^{c}	141.00 ± 6.69^{b}
P_P	–	–	–	–	131.7 ± 7.05^{c}	70.4 ± 3.83^{a}	202.3 ± 13.72^{d}	85.10 ± 6.64^{a}
P_N	–	–	–	–	73.5 ± 3.15^{b}	97.10 ± 9.11^{ab}	63.3 ± 2.12^{b}	231.30 ± 9.12^{b}
F-value	1185.66**	368.71**	254.06**	194.19**	179.01**	39.97**	90.73**	189.01**

Values are mean ± SE. Values followed by different alphabets show significant differences. ***F*-values to be significant at $P < 0.001$.

Table 2. Oviposition on two different G_N field taxes by *Z. bicolorata*

	Sets							
Taxes	*A*	*B*	*C*	*D*	*E*	*F*	*G*	*H*
100% G_N	252.70 ± 5.46^{b}	233.50 ± 9.86^{b}	60.60 ± 3.10^{b}	52.90 ± 2.78^{b}	176.70 ± 4.69^{b}	87.20 ± 11.20^{b}	111.20 ± 9.57^{b}	141.00 ± 6.69^{b}
Semi-G_N	53.73 ± 6.07^{a}	72.90 ± 7.16^{a}	22.70 ± 2.74^{a}	18.20 ± 2.50^{a}	20.50 ± 2.56^{a}	22.60 ± 2.73^{a}	17.20 ± 1.33^{a}	21.70 ± 2.86^{a}
F-value	593.6**	173.73**	84.03**	86.25**	856.22**	31.42**	94.61**	268.53**

Values are mean ± SE. Values followed by different alphabets show significant differences. ***F*-values to be significant at $P < 0.001$.

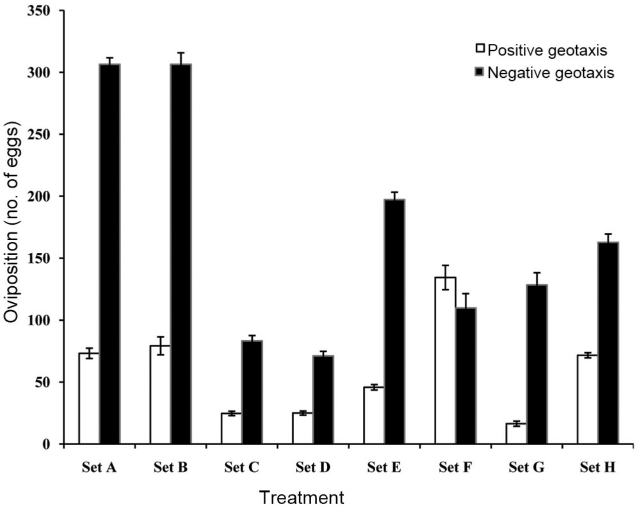

Figure 1. Geotactic ovipositional orientation in *Zygogramma bicolorata*.

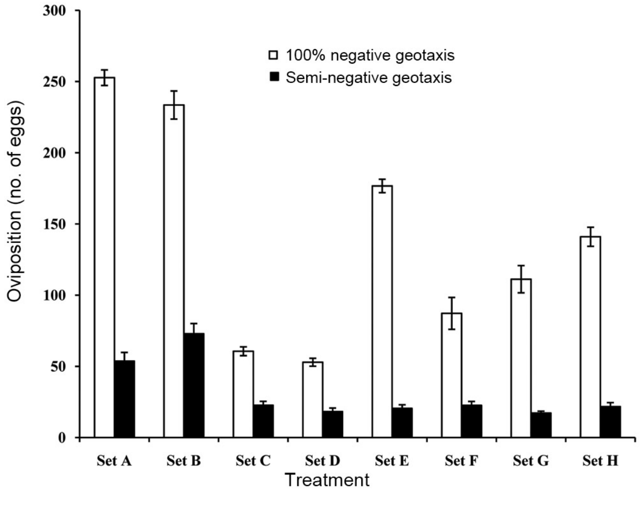

Figure 2. Pattern of oviposition by female *Z. bicolorata* in negatively geotactic substrata.

oviposited on P_NG_P. A maximum proportion of eggs (0.38) was laid on P_PG_N in set-up *G*, while a maximum proportion of eggs (0.56) was laid on P_PG_N in set-up *H*.

Orientation towards colour of substrata

The overall differences in colour preference were found to be statistically significant ($F = 31.08$; $P < 0.001$; d.f. = 5174). *Z. bicolorata* oviposited maximally on green-coloured substratum and minimum on black-coloured substratum (Figure 3).

Orientation towards texture of substrata

Maximum egg-laying by female *Z. bicolorata* was recorded on plastic substratum and minimum on cardboard (Figure 4). The overall differences in texture preference were also statistically significant ($F = 30.32$; $P < 0.001$; d.f. = 5174).

Discussion and conclusion

The results of the present study reveal maximum oviposition by female *Z. bicolorata* on negatively geotactic substrata. Further comparison within data for negatively geotactic taxes revealed a strong ovipositional preference for 100% G_N, than those perpendicular to the base (semi-G_N). Similar ovipositional preference for negatively geotactic substrata has also been reported in different insects, viz. *Propylea quatuordecimpunctata*[26], *Propylea dissecta* (Mulsant)[28] and *Lambdina fiscellaria*[29]. However, *Coccinella septempunctata* showed a preference for positive geotaxis[30].

The orientation preference of the beetle towards negatively geotactic substrata might be due to the negatively

Table 3. Proportion of number of eggs laid by *Z. bicolorata* in four combinations of taxes

	Sets							
	E		*F*		*G*		*H*	
Taxes	Proportion	Mean no. of eggs laid	Proportion	Mean no. of eggs laid	Proportion	Mean no. of eggs laid	Proportion	Mean no. of eggs laid
P_PG_P	–	–	0.01	9.73 ± 1.44^a	–	–	0.02	9.26 ± 1.24^a
P_PG_N	0.38	315.79 ± 6.47^b	–	–	0.38	220.82 ± 11.65^b	0.56	294.26 ± 7.18^c
P_NG_P	0.29	243.00 ± 6.70^a	0.36	244.20 ± 19.79^c	0.25	145.60 ± 10.30^a	–	–
P_NG_N	0.32	269.99 ± 5.99^a	0.21	144.43 ± 13.34^b	0.35	204.42 ± 11.43^b	0.42	222.66 ± 7.99^b
F-value	–	33.12**	–	72.65**	–	12.60**	–	563.63**

Values are mean ± SE. Values followed by different alphabet show significant differences. ***F*-values to be significant at $P < 0.001$.

Table 4. Order of preference for taxes by *Z. bicolorata*

Setups	Individual taxes	Combination taxes
A	$G_N > G_P$	*
B	$G_N > G_P$	*
C	$G_N > G_P$	*
D	$G_N > G_P$	*
E	$G_N > P_P > P_N > G_P$	$P_PG_N > P_NG_N > P_NG_P$
F	$G_P > P_P N > G_N > P_P$	$P_NG_P > P_NG_N > P_PG_P$
G	$P_P > G_N > P_N > G_P$	$P_PG_N > P_NG_N > P_NG_P$
H	$P_N > G_N > P_P > G_P$	$P_PG_N > P_NG_N > P_PG_P$

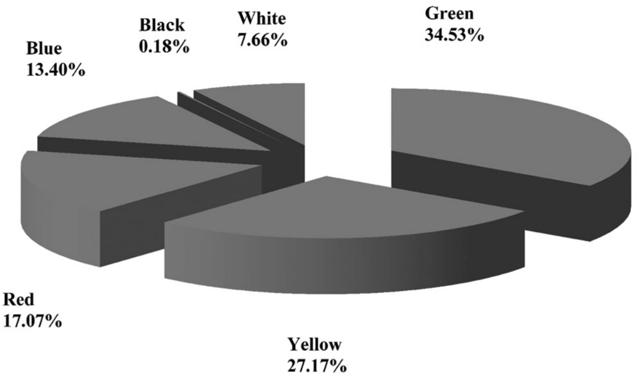

Figure 3. Ovipositional preference by females of *Z. bicolorata* for substrata of different colours.

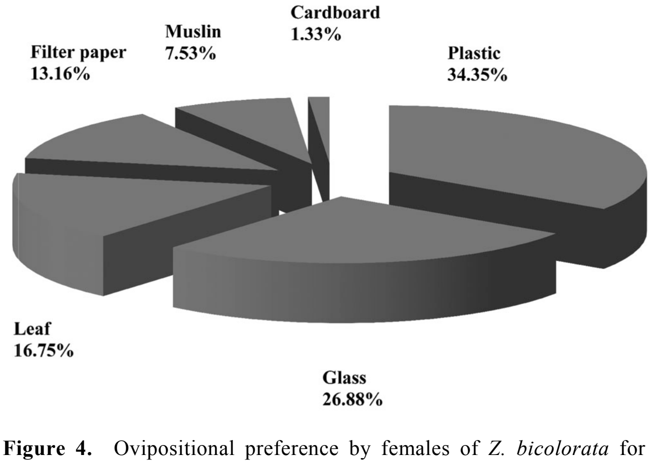

Figure 4. Ovipositional preference by females of *Z. bicolorata* for substrata of different textures.

geotactic foraging behaviour of the larvae. Third and fourth instars of *Z. bicolorata* feed mainly on the peripheral leaves and pollen of *Parthenium* plant. An aqueous extract of *Parthenium* pollen stimulated the food consumption of the first instar of *Z. bicolorata*[31]. Floral feeding by first instars is known to be especially prevalent in Chrysomelidae and Bruchidae[32].

Among phytophagous insects, larvae are often less mobile than ovipositing females[33]. Thus, larval survival mainly depends on the ovipositing female as habitat of the larvae is selected by the mothers only[34]. The selection of negatively geotactic substrata for egg-laying may help in decreasing the predation risk to eggs and provide a shaded and humid microclimate to the newly hatched larvae. This study reveals the lack of preference between positively phototactic and negatively phototactic substrata. The experiment was designed to examine the behaviour of the beetle in different photo fields. It was expected that *Z. bicolorata* will respond positively to the intensity and direction of light, while tempering the effect of directional pull of gravity. However, the results were contrary to this assumption. The finding gets support from a previous study on *P. quatuordecimpunctata*[26], whereas *C. septempunctata* preferred insolated areas[35] and *L. fiscellaria* showed positive phototaxis[29]. Experiments on a combination of taxes reinforced the results of taxes studied individually, that the negatively geotactic response was the most prominent. The preference for phototaxis largely depends on its alliance with a suitable geotaxis. More egg-laying was recorded on the substrates, which were combined with G_N. Though a deviation was observed in set-up *F*, negative phototaxis was slightly preferred over negative geotaxis. This ovipositional preference was probably due to the larger area exposed to the former. However, change in abiotic and biotic conditions may influence the choice of taxes by an organism[36].

Z. bicolorata oviposited maximally on the green-coloured substratum. The order of preference was green, followed by yellow, red, blue, white and black. However, no egg-laying was observed on the black-coloured substratum. The preference for green colour can be attributed to the fact that the preferred food of the insect is green in colour. The results of the present study corroborate with the previous findings in *C. septempunctata*[27] and *Coccinella transversalis*[37], i.e. green followed by yellow-coloured substratum over other colours. However, this finding contradicts the preference for red followed by green, yellow and blue by *P. quatuordecimpunctata*[25] and red followed by green, yellow, white, blue and black by *P. dissecta*[28].

Colours are perceived by the brain of an animal, depending on the particular sensory apparatus[38]. Responses to various colours are governed by the combined interaction of wavelength and intensity of light. Insects are known to change their behaviour according to the colour. For example, different chrysomelid beetles, viz. *Diabrotica barberi* Smith, *Diabrotica virgifera*, cabbage seed weevil, and *Ceutorhynchus assimilis* Paykull responded differently to different colours[39]. Ovipositing females of *Aedes aegypti* were found to be influenced by the colour of the ovitraps[40]. This behaviour of insects indicates their affinity to different colours.

It is evident from the results of the present study that *Z. bicolorata* oviposited maximally on plastic over other textures of the substrata, viz. glass, leaf, filter paper, cardboard and muslin. This probably indicates its preference for smooth over other rough substrata. The preference of plastic for oviposition over a smoother surface, like glass and rougher surfaces like leaves, filter paper, muslin and cardboard, may be ascribed to its comparative suitability to larval movement. As leaves have a rough surface, this may cause mortality in the newly hatched larvae and adults by lacerating their abdomen and may affect their foraging ability. However, smooth surfaces like glass may cause an individual to slip and fall-off[41]. It was earlier suggested that leaves bearing trichomes or hairs cause mortality[14] and reduce foraging ability[42]. This finding is supported by a similar preference of *P. quatuordecimpunctata*[7] and *P. dissecta*[28]. However, *C. septempunctata*[27] and *C. transversalis*[6] preferred host plant surface for oviposition, while *C. sexmaculat* preferred bolls, while *C. septempunctata* preferred a jar surface[23]. Egg laying by *C. septempunctata* has been recorded on soil, rock pieces[35] and on plants or plastic walls of experimental cages[24].

The above information on the ovipositional orientation will help predict the habitat choice and foraging patterns of the beetle. The outcome of the present study will contribute to improve mass multiplication and deduce the underlying microclimatic preferences.

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