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Plasticity in the Egg-Spacing Behavior of a Seed Beetle: Effects of Host Deprivation and Seed Patchiness (Coleoptera: Bruchidae)

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Egg-laying females of the seed beetle Callosobruchus maculatus *discriminate between egg-free and egg-laden seeds and produce a nearly uniform distribution of eggs among seeds. We examined plasticity in this trait in response to both an internal factor (level of host deprivation) and an environmental one (the spatial configuration of available seeds). Responses to each factor were measured in genetically divergent strains that show a relatively strong (S strain) or weak (B strain) tendency to spread eggs evenly among seeds. Following a modest (10-h) period of host deprivation, S-strain females distributed their eggs less uniformly among seeds; the proportion of females committing at least one oviposition "mistake" increased from 20 to 50%. Similarly, S-strain females distributed their eggs less uniformly if seeds were presented in multiple, discrete patches instead of in a single, large patch. The higher frequency of oviposition mistakes in the multiple-patch arena was caused in part by females maintaining a uniform distribution of eggs within patches but not among patches. In contrast, females from the "sloppier" B strain were unaffected by either host deprivation or resource dispersion. Responses to seed patchiness are discussed in relation to the role of learning in the egg-spacing behavior of* C. maculatus.

KEY WORDS: oviposition behavior; egg dispersion; plasticity; host deprivation; resource patchiness; *Callosobruchus maculatus.*

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INTRODUCTION

Oviposition preferences of insects are often determined by a complex interaction of factors that are both extrinsic and intrinsic to the egg-laying female (Miller and Strickler, 1984; Lewis *et al.*, 1990; Rosenheim and Rosen, 1991). For phytophagous species, extrinsic or environmental factors include the spatial configuration of potential host plants (Root and Kareiva, 1984), the chemical and physical characteristics of each plant (Renwick, 1989), and the number of eggs or larvae that may already occur on a plant (Roitberg and Prokopy, 1987). Intrinsic or internal factors that can affect egg-laying behavior include the female's genotype, her recent egg-laying experience, and her physiological condition (Papaj and Prokopy, 1989; Courtney and Kibota, 1990). Mangel and Roitberg (1989) illustrate how these factors interact in the fruit fly *Rhagoletis pomonella* (Walsh), where acceptance of a host depends on the fruit quality (if it is already infested or not), the female's "informational" state (if she has recently encountered mostly clean or infested fruits), and her physiological state (if the time since her last oviposition is short or long).

A major determinant of oviposition preference in the seed beetle *Callosobruchus maculatus* (F.) (Coleoptera: Bruchidae) is the presence of conspecific eggs on host seeds. Females lay eggs singly on the surface of dried seeds from several species of cultivated legumes. They avoid adding an egg to seeds that already bear eggs and, thus, produce a uniform dispersion of eggs among seeds (Utida, 1943; Avidov *et al.*, 1965; Mitchell, 1975). Once all available seeds bear eggs, females prefer seeds with few eggs over seeds with many eggs (Messina and Renwick, 1985; Wilson, 1988). This behavior reduces the frequency and intensity of larval competition within seeds.

Previous studies revealed substantial genetic variation in egg-spacing behavior among geographic strains of *C. maculatus* (Messina, 1989; Messina and Mitchell, 1989), perhaps as a result of concomitant variation in the relative costs associated with multiple larvae per seed (Mitchell, 1990; Messina, 1991). Here we extend these results by examining the plasticity of the behavior in response to both an internal factor (the level of host deprivation) and an environmental one (the spatial dispersion of potential host seeds). Specifically, we asked (1) Do deprived females show reduced discrimination between egg-free and egg-laden seeds, as predicted by both theoretical and empirical studies (e.g., Roitberg and Prokopy, 1983; Iwasa *et al.*, 1984; Mangel, 1987)? and (2) Does the female's ability to spread eggs uniformly among seeds decline when seeds are distributed in multiple patches instead of a single patch (cf. Cain *et al.*, 1985; Bell, 1990)? By testing females from genetically divergent strains, we also examined whether strain differences observed under one set of conditions are maintained across a range of environments (Bell and Tortorici, 1987).

MATERIALS AND METHODS

We used two beetle strains that differ genetically in egg-laying behavior (Messina, 1989; Messina *et al.*, 1991). Females from the S strain, which was collected in India, produce egg distributions that are completely uniform or nearly so, at least until all available seeds bear two or more eggs (Thanthianga and Mitchell, 1990). Females from the B strain, which is derived from Brazil, are more variable, and often produce egg distributions that are closer to random than to uniform. Strain histories and rearing methods are provided by Messina and Mitchell (1989). We used mung bean, *Vigna radiata* (L.) Wilczek, as the experimental host because its seed coat permits high visibility of eggs. We used only smooth, intact seeds of similar size in order to minimize variation in seed quality. Egg distributions tend to be more uniform on mung bean than on larger hosts, but the respective differences between the S and the B strains are maintained across host species (Messina and Mitchell, 1989). Experiments were conducted in a dark incubator at 28 ± 1°C.

Host Deprivation Experiments

We collected females for each experiment within 1 h of adult emergence (older adults had been sieved out of the cultures earlier), so that they had no egg-laying experience. Each female was paired with a newly emerged male in an empty, 5-cm petri dish for 4 h, after which males were discarded. Control females were then individually assayed for egg-laying behavior immediately. Deprived females were retained in their dishes without seeds for an additional 10 h and then tested. Control and deprived groups were thus tested 4–5 and 14–15 h after adult emergence, respectively.

In Experiment I, each female was placed in a 5-cm petri dish containing 16 seeds for 24 h. We quantified egg dispersion using the uniformity index, U (Messina and Mitchell, 1989). Briefly, this index is derived from the number of "mistakes" a female makes in distributing her eggs, which is defined as the minimum number of eggs that must be transferred between seeds in order to transform the observed distribution of eggs into a discrete uniform one. This observed number of mistakes is then compared to the expected number of mistakes that would be committed by a random (Poisson) female laying the same number of eggs on 16 seeds. $U =$ (expected mistakes − observed mistakes) ÷ expected mistakes. The index usually ranges from 0, which indicates that a female distributed her eggs randomly, to 1, which indicates complete uniformity. If a female tended to clump her eggs on seeds, $U < 0$.

We tested approximately 45 females in each of the four treatments (2 strains × 2 levels of deprivation). Females that laid fewer than five eggs (probably because of mating failure) were eliminated from the analysis. Two-way ANOVA was used to analyze the effects of beetle strain and deprivation on both egg dispersion and the number of eggs laid (Wilkinson, 1988). To satisfy assumptions of ANOVA, we used the transformation, $(1 + U)/2$, to place all U values between 0 and 1 (no raw score was < -1) and then applied the arcsine-square root transformation.

Experiment II was similar to the first except that we measured how control and deprived females distributed their first few eggs on seeds, when the effect of deprivation is presumably strongest. Control and deprived females were provided only six seeds and were allowed to oviposit for only 3 h. The small number of eggs laid during this period precluded using an index of egg dispersion. Instead, we simply calculated the percentage of females that made an oviposition mistake, which in this assay meant that a female added a second egg to a seed when at least one egg-free seed remained available. We used only the S strain for this experiment (50 females per treatment) because of the lack of response to deprivation by the B strain in Experiment I (see Results). A G test of independence was used to compare the percentages of females committing mistakes in the two treatments (Sokal and Rohlf, 1981); statistical power was estimated from Appendix 3 of Wickens (1989).

Experiment III directly examined whether deprivation affected discrimination between egg-free and egg-laden seeds, as females were given a choice between the two kinds of seeds at the start of the experiment. We first obtained egg-laden seeds by placing 20 females from the appropriate stock culture into each of eight, 9-cm petri dishes containing about 250 seeds. After 3 h, we collected all seeds bearing one egg. Egg-laden seeds were then stored with an equal number of egg-free seeds at 8°C for 24–48 h until needed for the experiment. Each test female (control or deprived) was placed in a dish containing three egg-free seeds and three egg-laden seeds for 1 h. We again compared the percentage of females that committed a mistake, i.e., added an egg to an egg-laden seed when one or more of the egg-free seeds had not yet received an egg. We tested approximately 75–80 S-strain females/treatment.

Seed Patchiness Experiment

We compared egg distributions produced by females presented seeds in a single patch or in multiple patches. Females were tested individually in an arena composed of two square, Plexiglas sheets (36 × 36 cm) sandwiched above and below a wooden frame, which provided an interior depth of 2 cm. Each arena contained 16 seeds, arranged either as a single, center-patch or in four corner-patches of four seeds/patch (Fig. 1). The distance between the centers of adjacent seeds within any patch was 1 cm; the distance between the centers of adjacent patches in the multiple-patch arena was 30 cm. Because the length of the largest *C. maculatus* female is about 4 mm, the distance between adjacent

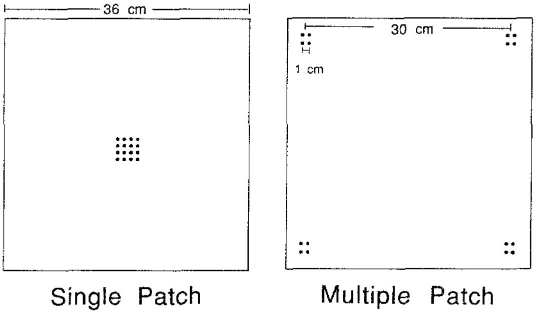

Fig. 1. Arrangement of 16 available seeds into a single patch or multiple patches in an arena.

patches in the multiple-patch arena typically represented over 75 female body lengths. Seed arrays were formed by attaching each seed to the lower Plexiglas sheet with a small dab of glue. The necessary amount of glue covered little more than the portion of the seed already in contact with the Plexiglas.

We tested approximately 25 females in each of four treatments: 2 strains × 2 spatial configurations. Newly emerged, mated females were collected as described above. Each female was released into the center of an arena and allowed to distribute her eggs on the 16 available seeds until death, which, at 28°C, occurred 3–7 days after adult emergence and before any eggs hatched. We recorded where each egg was laid and estimated egg dispersion using the U index described above. We used two-way ANOVA to assess the effects of beetle strain and seed patchiness on lifetime realized fecundity and performed separate, one-way analyses of variance to analyze the effect of seed patchiness on egg dispersion within each strain.

RESULTS

Effects of Host Deprivation

A 10-h period of deprivation had a moderate but significant influence on egg-spacing behavior. In Experiment I, egg dispersion varied as expected between beetle strains ($F_{1,163} = 144.95$, $P < 0.001$), with distributions produced by S-strain females much more uniform than those of B-strain females (Table I). The effect of host deprivation was also significant ($F_{1,163} = 6.04$, $P = 0.02$), as deprived S-strain females produced egg distributions that were less uniform than those of control females. In the B strain, however, deprivation had no apparent effect on egg-laying (Table I). This asymmetry is suggested by the nearly significant interaction between the effects of strain and deprivation

Table I. Mean Number of Eggs Laid and Mean Dispersion Index (U) of *C. maculatus* Females that Were Subjected to 0 or 10 h of Host Deprivation

Strain	Deprivation (h)	No. of eggs (±SE)	U (±SE)[a]	No. of females
S	0	16.8 ± 0.8	0.93 ± 0.03	37
S	10	18.4 ± 0.7	0.85 ± 0.03	42
B	0	19.8 ± 0.7	0.38 ± 0.04	44
B	10	22.1 ± 0.9	0.38 ± 0.05	44

[a] A U value of 1 indicates a completely uniform egg dispersion; a value of 0 indicates a random distribution.

on egg dispersion ($F_{1,163} = 3.46$, $P = 0.06$). We therefore used only the S strain for Experiments II and III.

Differences between control and deprived S-strain females in Experiment I are more evident when we compare the percentages of females that committed at least one mistake (i.e., did not achieve a completely uniform egg dispersion). Only 19% of 37 control females committed a mistake, as opposed to 50% of 42 deprived females ($G = 8.60$, df = 1, $P < 0.005$). Every B-strain female committed at least one mistake in distributing her eggs.

B-strain females laid more eggs during the 24-h assay in Experiment I than S-strain females did (Table I; $F_{1,163} = 7.02$, $P = 0.01$). Deprived females laid a slightly greater number of eggs than control females did, but this effect was not significant ($F_{1,163} = 1.81$, $P = 0.18$); there was also no interaction between strain and deprivation ($F_{1,163} = 0.24$, $P = 0.62$). The relatively minor variation among treatments in the number of eggs laid does not account for the variation in egg dispersion; egg number and dispersion were uncorrelated within each treatment (r values ranged from 0.01 to 0.24; df = $N - 2$; all P values >0.10).

In Experiment II, deprived females from the S strain again tended to be "sloppier" in their egg-laying than control females. Only 18% of 44 control females committed an oviposition mistake (i.e., added a second egg to a seed when an egg-free seed was still available), whereas 31% of 51 deprived females did so. This difference, which follows the trend in Experiment 1, was not significant ($G = 2.22$, $0.10 < P < 0.25$), but the test's power to detect a true difference of this magnitude was only ≈ 0.3. Control females did lay fewer eggs than deprived females did over the 3-h oviposition period ($\bar{X} \pm \text{SE} = 5.6 \pm 0.3$ and 6.7 ± 0.3 eggs, respectively; $t = 2.75$, $P < 0.01$), but the difference in egg number again could not account for the difference in mistake frequency. If we consider only females that laid ≤ 6 eggs (and thus never lacked an egg-free seed during the assay), the trend remained the same; 25% of control females (N = 28) committed at least one mistake, versus 46% of deprived females ($N = 24$; $G = 2.49$, $0.10 < P < 0.25$; statistical power ≈ 0.35).

Experiment III provided females with a direct choice between egg-laden and egg-free seeds, with the eggs on egg-laden seeds derived from females other than the test female. Most females laid 2–4 eggs during the 1-h test period (range, 1–6). The percentage of females committing a mistake (adding an egg to an egg-laden seed when an egg-free seed was available) was 13% among control females ($N = 68$) and 24% among deprived females ($N = 79$). This difference was marginally significant ($G = 2.84$, $0.05 < P < 0.10$) and, again, conforms to the results of Experiments I and II.

Effects of Seed Patchiness

The seed-patchiness experiment examined how each female distributed her eggs among 16 seeds over her lifetime. The S and B strains differed markedly in their lifetime realized fecundity ($F_{1,90} = 91.05$, $P < 0.001$). S-strain females typically produced egg densities of about 2 eggs/seed, whereas B-strain females often laid nearly 4 eggs/seed (Table II). The lower fecundity of the S strain was caused by two factors: a lower potential fecundity in this strain (Messina and Mitchell, 1989) and a tendency for S-strain females to "withhold" eggs once all seeds bear 2–3 eggs (Thanthianga and Mitchell, 1990; Messina, 1991). We detected no effect of seed patchiness on fecundity ($F_{1,90} = 0.05$, $P = 0.83$), nor was there an interaction between strain and seed patchiness ($F_{1,90} = 0.23$, $P = 0.64$).

Because of the large differences in egg densities produced by S- and B-strain females in this experiment, we analyzed the effect of seed patchiness on egg dispersion separately for each strain. Seed patchiness had a significant effect on mean egg dispersion in the S strain ($F_{1,46} = 5.00$, $P = 0.03$), as females presented with seeds in multiple patches laid eggs less uniformly than females presented with a large, single patch (Table II). The spatial configuration of seeds had no effect on B-strain females ($F_{1,44} = 0.02$, $P = 0.89$). S-strain females from each type of arena again distributed their eggs much more uniformly than the corresponding B-strain females did (Table II). The percentage of S-strain

Table II. Mean Number of Eggs Laid and Mean Dispersion Index (U) of *C. maculatus* Females Provided 16 Seeds in a Single Patch or in Multiple Patches

Strain	Patchiness	No. of eggs (±SE)	U (±SE)[a]	No. of females
S	Single patch	33.1 ± 2.5	0.91 ± 0.03	23
S	Multiple patch	33.8 ± 1.8	0.80 ± 0.04	25
B	Single patch	62.0 ± 3.4	0.57 ± 0.03	23
B	Multiple patch	60.0 ± 3.6	0.58 ± 0.04	23

[a] As in Table I, footnote *a*.

females committing at least one mistake in distributing their eggs was 48% ($N = 23$) when seeds were presented in a single patch, as opposed to 76% ($N = 25$) when seeds were presented in multiple patches ($G = 4.13$, $P < 0.05$). In the B strain, 22 of 23 females produced at least one oviposition mistake when seeds were presented in a single patch, as did all females presented seeds in multiple patches.

The egg-dispersion scores and the mistake frequencies are based on how each female spread her eggs over all seeds. Less uniform egg-laying by S-strain females in the multiple-patch arena may simply indicate a tendency to lay eggs uniformly within a patch but not among patches. Figure 2 illustrates two actual egg distributions produced by females that committed a mistake in distributing their eggs over all seeds, yet achieved the most uniform distribution possible within each patch. Female A, for example, added a fourth egg to a seed when six other seeds in the arena still bore only two eggs, but all seeds in the patch containing the four-egg seed received three eggs. If mistakes are "counted" only within patches, the percentage of females making at least one mistake was 48% in both the single- and the multiple-patch arenas (11 of 23 versus 12 of 25, respectively).

The effect of seed patchiness on egg-laying is further illustrated by the variation in egg density among patches in the multiple-patch arena. S-strain females often distributed their eggs so that separate patches differed by as many as 3–4 eggs/patch (Fig. 3). Female A in Fig. 2, for example, laid 13 eggs in the lower-left patch, versus 9 eggs in the upper-right patch. For comparison, we can divide the single-patch array into four quadrants and estimate the maximum differences in egg density among the four-seed quadrants. Most S-strain females presented with a single patch of seeds distributed their eggs so that this difference between quadrants was only 1–2 eggs (Fig. 3). The average range in

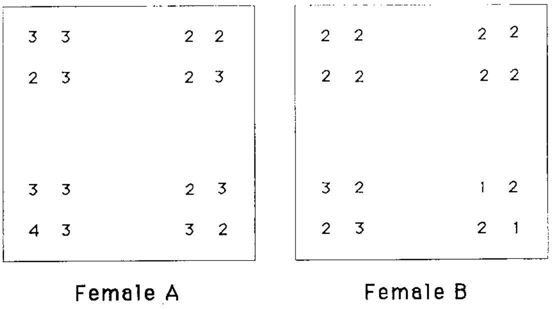

Fig. 2. Number of eggs laid on each of 16 seeds by two S-strain females of *C. maculatus* in the multiple-patch arena. Each female committed at least one "mistake" in failing to spread her eggs uniformly among all seeds but distributed eggs in the most uniform way possible within each patch.

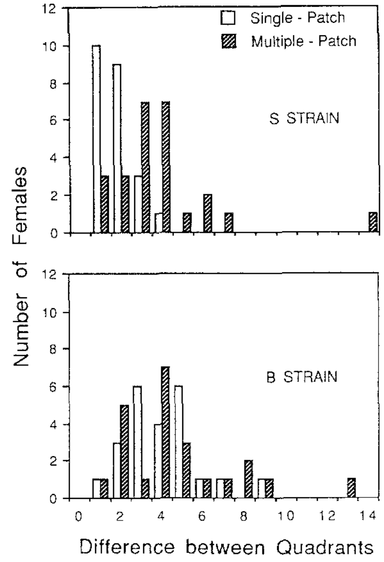

Fig. 3. Maximum differences in the number of eggs laid per four-seed quadrant when *C. maculatus* females were presented seeds in a single patch or in multiple patches.

egg density between patches in the multiple-patch arena was significantly higher than the corresponding range between quadrants in the single-patch arena (3.84 versus 1.78, respectively; Mann–Whitney U-test, $U_s = 474.5$, $P < 0.05$). The two treatments remain significantly different even if we omit an unusual female that produced a difference of 14 eggs between patches in the multiple-patch arena (Fig. 3; $U_s = 451.5$, $P < 0.05$). B-strain females distributed their eggs so that patches or quadrants often differed by 4–5 eggs (Fig. 3); the mean range in egg density between separate patches was only slightly higher than the corresponding range for quadrants within a patch ($\bar{X} = 4.69$ versus 4.04, respectively; $U_s = 286.5$, $P > 0.05$).

As noted above, one S-strain female in the multiple-patch arena produced a difference of 14 eggs between the patch with the most and that with the fewest eggs. This female simply failed to exploit one of the patches, perhaps because she never discovered it. Every other S- or B-strain female, however, laid at least 1 egg in each patch or quadrant, and 90 of the 94 test females laid at least 1 egg on every seed. The differences in egg dispersion and mistake frequency between the two groups of S-strain females therefore cannot be explained by a failure to locate seeds in the multiple-patch arena.

DISCUSSION

A 10-h period of deprivation caused S-strain females to commit more mistakes and produce a less uniform dispersion of eggs during the 24-h test period. This result may not be surprising, since 10 h represents a nontrivial fraction of the female's entire oviposition period of 3–5 days at 28°C. Avidov *et al.* (1965) imposed a drastic period of host deprivation (96 h) on groups of females from the closely related species, *Callosobruchus chinensis* (L.), and observed that eggs were significantly aggregated on seeds during 6 h of subsequent oviposition. They speculated that deprived females may abandon the typical habit of laying eggs singly and deposit several eggs sequentially on the same seed. The short-term assays of Experiments II and III indicated that females continued to lay eggs singly following the more modest deprivation in this study.

A general decline in the selectivity of egg-laying females has been found in several insects following host deprivation (e.g., Singer, 1982; Fitt, 1986; Odendaal and Rausher, 1990). Increased acceptance of less preferred hosts may be expected in species where the female lays less than her full complement of eggs per oviposition bout, and her load of eggs varies continuously with the availability of hosts (see discussion by Barton Browne *et al.*, 1990). A *C. maculatus* female emerges from a seed with about eight mature oocytes, and even in the absence of hosts, mature oocytes continue to accumulate in her reproductive system for at least 2 days (Credland and Wright, 1989; Wilson and Hill, 1989). Distension of the bursa or oviducts after 10 h of deprivation in this study may have led to a higher probability of acceptance of egg-laden seeds, although the deprivation was not so severe as to cause "dumping" of eggs on the container or other unsuitable substrates (Wilson and Hill, 1989; Messina, 1991). Alternatively (or additionally), control and deprived females may search differently among hosts (Bell, 1990); deprived females, for example, may inspect fewer seeds between oviposition bouts and, hence, fail to encounter some egg-free seeds. Because all test females had no egg-laying experience, the effect of deprivation cannot be explained by females "forgetting" how to discriminate between egg-laden and clean seeds or by habituation to egg-laden seeds (Roitberg and Prokopy, 1983).

Whatever the mechanism causing a higher frequency of mistakes by deprived, S-strain females, no effect of deprivation was apparent in the B strain. These results, plus those from the seed-patchiness experiment, suggest that behavioral plasticity may itself be strain specific and can be considered to represent a genotype × environment interaction at the level of divergent strains. The lack of response in the B strain was not due to females already laying eggs randomly without deprivation or in the single patch. Random females would yield a mean U index close to zero, with equal numbers of individuals receiving positive and negative scores. Mean egg dispersion was $\gg 0$ for both B-strain treatments in Experiment I (Table I) and was even closer to uniformity in the seed-patchiness experiment ($\overline{U} > 0.5$; Table II), when the 16 seeds were presented in an evenly spaced array instead of a loose pile. Nevertheless, the probability of committing an oviposition mistake may already be sufficiently high among B-strain females that a longer period of deprivation (or a greater distance between patches) is necessary to decrease the uniformity of egg distributions further. Despite the asymmetrical responses of the two strains to deprivation and seed patchiness, their respective egg-laying patterns did not converge; S-strain females in the multiple-patch arena, for example, did not become as ''sloppy'' as B-strain females in the single-patch arena (cf. Bell and Tortorici, 1987).

The spatial configuration of seeds affected the egg-laying pattern of S-strain females and led to relatively high variation in egg density among patches in the multiple-patch arena (Table II and Fig. 3). Several females laid eggs uniformly within patches but not among patches (Fig. 2). Perhaps females were comparing egg loads on seeds within a patch but did not retain this information when moving between patches (Mangel, 1990). Credland and Wright (1990) found that *C. maculatus* females were more discriminating when clean seeds and seeds bearing the putative marking pheromone were interspersed rather than in separate quadrants. Since mixing of seeds increases the chances that marked and control seeds are encountered in succession, they interpreted this result to mean that females compare the egg load on each seed with that of the seed visited previously (Mitchell, 1975; Thanthianga and Mitchell, 1990). In contrast, Wilson (1988) suggested that memory was not involved in egg-laying by *C. maculatus;* females instead may use an ''absolute rule,'' where the probability of seed acceptance declines with each increase in egg density (these probabilities of seed acceptance can of course be affected by host deprivation). While sensitivity to the spatial configuration of hosts suggests that females are indeed incorporating information from previously visited seeds, direct tests are needed to assess the role of learning in the egg-spacing behavior of *C. maculatus*.

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