

LIMITED EVIDENCE FOR SIZE-BASED DISCRIMINATION OF OVIPOSITION SITES IN *Callosobruchus maculatus* (COLEOPTERA: BRUCHINAE)

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ABSTRACT

Because variation in host quality and levels of intraspecific competition have been shown to affect growth, survival, and fecundity in a large number of parasitoid and obligate internally feeding granivore species, it is expected that selection will favour those females that are able to discriminate among potential hosts. Previous studies on the bruchid beetle *Callosobruchus maculatus* (F.) have shown that females lay more eggs on large seeds than small seeds. These studies, however, have typically presented females of a single strain with seeds that differed markedly in size. Here, we test the ability of females of two strains, which differ in their larval competition strategies, to discriminate among incremental levels of “small” versus “large” seeds. Based on previous studies, we predicted that females of both strains would exhibit a preference for larger seeds, which would increase as the difference in size increased. We also predicted that contest strain females would exhibit greater levels of discrimination than scramble strain females. Contrary to our expectations, we found low levels of discrimination for most strain × size difference combinations, and our statistically significant findings were partially due to high sample sizes and low variation in oviposition preferences. Our data on the mass and fecundity of female offspring potentially shed a light on these patterns: females from “large” seeds rarely had mean body mass or fecundity values significantly greater than those from paired “small” seeds. We advocate that future studies consider female oviposition decisions when presented with subtle variation in host quality.

Keywords: *Bruchid, Coleoptera, Fitness, Granivore, Oviposition, Preference*

1. INTRODUCTION

Insect parasitoids are expected to experience strong selection pressure to discriminate among hosts of varying quality because larvae exhibit obligatory development in a single host with no option to disperse [1]. Consequently, the mother’s choice of host ultimately determines the conditions experienced during development. A number of studies have demonstrated that females will preferentially oviposit on large, pristine hosts of the highest quality [2,3]. Optimal host selection should result in offspring with larger mass, higher survivorship and greater fecundity [4]. Therefore, natural selection should act to sharpen discrimination ability so that female fitness is maximized.

Seed beetles (Coleoptera: Chrysomelidae: Bruchinae), being obligate internally feeding granivores, possess a number of characteristics in common with parasitoids [3, 5, 6]. Females oviposit on the testa of legume seeds, which serve as a discrete patch for developing larvae [7,8]. Pupation occurs within the seed and adults mate soon after emerging from the host. The oviposition behaviour [9,10] and, more specifically, host-size discrimination ability of *Callosobruchus maculatus* (F.) has been the subject of considerable attention [10-12,3,4]; see also [13] for similar work with *C. chinensis*. Results from such experiments consistently indicate that female *C. maculatus* prefer to lay eggs on larger seeds. However, in the experiments in which females are presented with a choice between two groups of seeds, size differences vary between 85% [3], over 100% [4], or with size classes so large that differences ranged from 24% to 300% [12]. Other work involved weighing seeds after oviposition and results showed a preference for large seeds when size differences varied from 4% to 84% [2,11]. Thus, it is not known at precisely what resolution a

female can discriminate between hosts of different sizes. Previous tests are also confounded by the fact that there are several geographical strains of *C. maculatus* and each strain exhibits unique behavioural traits [11]. In the present experiment, we tested two strains of *C. maculatus* reared on seeds of two legume species for host-size discrimination ability. Our objective was to explicitly test whether females would choose between different-sized seeds with progressively greater differences in mass.

Based on previous studies, we had three a priori predictions regarding host size discrimination by females and the resulting fitness consequences of their decisions. First, we predicted that female bruchids would discriminate between different sized seeds when the mass difference was sufficiently great to convey a fitness advantage to her offspring. Second, we predicted that contest strain female beetles (i.e., exhibit interference competition within seeds) reared on mung would demonstrate a greater level of discrimination than scramble strain females (i.e., avoid competition and share resources) reared on the larger adzuki. Finally, provided that host size discrimination did indeed occur, we predicted that a fitness benefit would be experienced by the offspring generation such that female offspring emerging from larger seeds would have greater body mass and/or exhibit increased fecundity.

2. MATERIALS AND METHODS

Two related experiments were performed using two strains of *C. maculatus*, 'iQ' (hereafter contest strain) and 'hQ' (hereafter scramble strain). The contest strain was established from mung (*V. radiata* (L.) Wilczek) and black gram (*V. mungo* (L.) Hepper) in Tirunelveli, India in 1979 [12] and has been reared continuously on mung. The scramble strain was collected from imported broad beans (*Vicia faba* L.) in 1992 by M. Tuda (M. Tuda, pers. comm., 2002), and has since been cultured on adzuki. Insects were reared in 24 h darkness at $28 \pm 1^\circ\text{C}$, $48 \pm 3\%$ RH.

To test the effects of seed size on female oviposition decisions, we established size-difference treatments for potential host mung (contest strain) and adzuki (scramble strain) seeds. Treatments consisted of two size classes of bean that differed in mass by 7%, 14% or 21% for mung, and 14% or 28% for adzuki, replicates. Interference competition is common among larvae of the contest strain [8,14], with small mung seeds rarely producing more than one adult. Based on such observations, it was expected that contest strain females would exhibit strong discrimination. Because more than one larva of the scramble strain develops in an adzuki seed almost without exception, we expected that scramble strain females would be less likely to discriminate between small differences in size. Therefore, we employed larger size differences overall, keeping one size-difference treatment (i.e., 14%) common between the two strains. Finally, we retained the two strains on their natal species, as opposed to using a common host type (e.g., cowpea), because of the issues associated with interpreting (a lack of) discrimination of different sized seeds of a novel host. Mean (\pm SD) masses of the size classes for the mung and adzuki treatments are presented in Table 1.

To ensure that emerging adults were virgins, host seeds from the stock culture were haphazardly selected and isolated in 1.5 ml microcentrifuge tubes shortly before expected adult emergence. Tubes were checked every 12 h and only adults less than 12 h old were used for experiments. Upon emergence, individual females were paired with a single male in a small Petri dish (35 mm \varnothing). Matings typically occurred almost immediately (i.e., <10 min). For the contest strain, the female was then placed in a new Petri dish (35 mm \varnothing) with 4 large and 4 small seeds from either the 7%, 14% or 21% size-difference treatments. Females were allowed to oviposit for 24 h with a brief interruption at 12 h for an intermediate egg count. After 24 h, the female was removed and the eggs counted. Seeds with eggs were isolated in 1.5 ml microcentrifuge tubes and placed in a growth chamber until adults emerged in the progeny generation. Fifty females were used for each treatment. The same protocol was followed for scramble strain beetles on adzuki, except for the size-difference treatments (i.e., 14% or 28%, rather than 7%, 14%, or 21%). For both strains, females that did not lay any eggs within 24 h were excluded from subsequent analyses.

In the fecundity experiment, we tested the effects of parental oviposition decisions on the fitness of offspring. Cultures of seeds with the isolated progeny generation were checked every 12 h, beginning several days before we expected the first emergence, thus only adults less than 12 h old were used in the experiment. Emerging adults of the progeny generation were mated within each size class of the size-difference treatments. Offspring were inbred

within their sib-group or outbred with another individual from the same size class depending on availability of mates. There were no differences in the number of eggs laid by inbred and outbred individuals from the same size class for all class \times strain combinations (generalized linear model with Poisson errors; all $P > 0.05$), therefore data within size classes were pooled for analysis. Females were weighed on a microbalance and paired with a male in a 100 mm Petri dish (100 mm diameter) with 100 haphazardly selected seeds. Mating typically occurred almost immediately and the male was subsequently removed. Females were allowed to oviposit for 24 h, after which the total number of eggs was counted. Although this aspect of the experiment precluded establishing target sample sizes a priori, because we were limited to female offspring of the parental generation that would mate and lay eggs, sample sizes were reasonably balanced for large vs. small seed pairs within the same strain \times size-difference combination (Table 2).

We evaluated female discrimination ability by calculating the proportion of eggs oviposited on large seeds [3]; proportions were logit transformed and subject to one-tailed t -tests. For the offspring generation, we used linear models to analyze the effects of size-difference treatment (7%, 14% and 21% for mung; 14% and 28% for adzuki), seed size (large vs. small), and the interaction between size-difference treatment and seed size on natural log transformed body mass. Generalized linear models (GLM) with quasi-Poisson errors were used for analyses of the effects of the same model terms on fecundity (i.e., number of eggs laid after 24 h). Finally, to investigate possible changes in mass-corrected fecundity [8], we first conducted separate GLMs with quasi-Poisson errors on the relationship between body mass and fecundity for each strain to obtain residual fecundity values for females. We then followed the approach used for analyzing body mass (see above), using these residual fecundities as the response variable. GLMs were fit using R 2.9.2 [15].

3. RESULTS

We found only limited evidence for seed size discrimination by parental females. Female contest strain beetles significantly discriminated between varying sizes of mung when “small” and “large” beans differed in mass by 21% (Table 3). Contest strain females laid a significantly greater proportion of eggs on large mung beans than on small mung beans at the 12 and 24 h counts for the 21% size difference treatments. Females laid a significantly greater proportion of eggs on large mung beans after 12 h for the 7% size difference treatment; however, that proportion decreased after 24 h and the difference between the two groups was no longer significant (Table 3). Contest strain females did not lay a significantly greater proportion of eggs on large mung beans than on small at 12 or 24 h for the 14% size difference treatment. The overall tendency for females to lay a greater proportion of eggs on the larger group of seeds (Table 3) was corroborated by a significant positive relationship between mung bean mass and number of eggs per seed after 24, but not 12, h (Fig. 1).

Scramble strain females did not exhibit significant discrimination between “small” and “large” adzuki in either size difference treatment at either time count (Table 3). There was evidence for a marginally significant preference for large adzuki seeds after 24 h in both size difference treatments (Table 3). Furthermore, we did not observe a positive relationship between mean adzuki mass and number of eggs per seed at either 12 or 24 h (Fig. 2). The lack of a relationship in Fig. 2 indicates that scramble strain females have little ability to discriminate between seeds, even when there is a large difference in mass. Alternatively, it may indicate that scramble strain females do not gain measurable benefits from ovipositing on larger seeds.

There was no effect of size-difference treatment ($t_{1,137} = 0.91$, $P = 0.37$) or seed size (i.e., large vs. small; $t_{1,137} = 0.80$, $P = 0.42$) on mass of contest strain females (i.e., daughters of the generation presented with different-sized mung). Additionally, there was no interaction between the two factors ($t_{1,137} = 0.30$, $P = 0.77$) (Fig. 3a). Conversely, there was a significant effect of seed size ($Z_{1,137} = 3.23$, $P = 0.0009$), and a marginally significant interaction between size-difference treatment and seed size ($Z_{1,137} = 1.71$, $P = 0.087$), on fecundity. The main effect of size-difference treatment was not significant ($Z_{1,137} = 0.79$, $P = 0.43$). In general, females that emerged from larger seeds laid more eggs than those emerging from smaller seeds (Fig. 4a). Curiously, the difference in fecundity was the greatest in the 7% size difference treatment (Fig. 4a). Finally, there was limited evidence for differences in mass-

corrected fecundity, with a marginally significant effect of seed size ($t_{1,137} = 1.68$, $P = 0.095$), no effect of size-difference treatment ($t_{1,137} = 0.20$, $P = 0.84$), and no interaction between the two factors ($t_{1,137} = 0.89$, $P = 0.38$). With regard to the effect of seed size, there was a tendency for daughters from larger seeds to lay more eggs for their body mass.

There was a marginally significant interaction between size-difference treatment and seed size on body mass of scramble strain females emerging from adzuki ($t_{1,92} = 1.89$, $P = 0.062$). The main effect of size-difference treatment was also significant ($t_{1,92} = 3.13$, $P = 0.0024$), whereas that of seed size was not ($t_{1,92} = 1.57$, $P = 0.12$). Females emerging from the 28% size-difference treatment tended to have greater mass than those emerging from the 14% size-difference treatment; within the former treatment, females emerging from large seeds were heavier than those emerging from small seeds (Fig. 3b). However, these mass differences did not translate into differences in fecundity: size-difference treatment ($Z_{1,92} = 0.64$, $P = 0.52$), seed size ($Z_{1,92} = 1.03$, $P = 0.30$), and the two-way interaction between the factors ($Z_{1,92} = 1.02$, $P = 0.31$) were all nonsignificant (Fig. 4b). Finally, there was no evidence for differences in mass-corrected fecundity, with no effect of size-difference treatment ($t_{1,92} = 1.66$, $P = 0.10$) or seed size ($t_{1,92} = 0.29$, $P = 0.77$), and no interaction between the factors ($t_{1,92} = 0.52$, $P = 0.60$).

4. DISCUSSION

In the present experiment, we hypothesized that (i) female bruchid beetles would exhibit some level of host size discrimination, and (ii) this discrimination behaviour would increase fitness through increased fecundity of the offspring generation. Previous work indicates that female bruchids will discriminate among hosts of variable size, but to what degree they are able to do so is largely unknown. Here, we observed discrimination at the extreme range of host sizes for contest strain beetles reared on mung. This discrimination was accompanied by very limited evidence for fitness-related benefits. Scramble strain beetles demonstrated statistically significant discrimination ability, although the magnitude of this discrimination was small. Additionally, the discrimination resulted in a modest body mass, but no fecundity, increase.

To refine previous studies investigating related phenomena in bruchid beetles, we presented females with a smaller range of differences between ‘small’ and ‘large’ seeds. The 21% size difference treatment for mung and 28% size difference treatment for adzuki represented the maximum ranges in mass consistently available to us commercially. Seeds larger and smaller in mass were not found in sufficient number to create size classes. Although extremes of 300% difference in mass (e.g., as used in [12]) undoubtedly exist, smaller differences in mass are likely encountered with much greater frequency in grain stores. For example, a mass of 51.2 ± 12.3 g (mean \pm SD) was reported for seeds of a rain forest tree (*Beilschmiedia bancroftii*) attacked by a mammalian seed predator (*Uromys caudimaculata*) [16]. Even if we choose the most extreme values represented by the ~68% of individuals contained within that range, and calculate the size difference as we did for our treatments (i.e., $[63.5 - 38.9]/38.9$), we obtain a value of 63%. Most pairs of seeds drawn at random from that sample would differ by less than that magnitude. Based on such observations (see also [17]), we expected more refined discrimination ability from females in our experiments. However, our results for mass and fecundity of female offspring corroborate limited discrimination ability. Females that oviposited on larger seeds when presented with relatively small differences in mass did not consistently gain a significant fitness benefit. We note that the finding of scramble strain females laying a “significantly” greater proportion of eggs on larger adzuki after 24 h is partly a function of low variation in preference and high sample size; proportions of eggs on large seeds were only slightly more than 0.50 after 24 h (Table 2). Scramble strain females were expected to exhibit less discrimination because larvae do not compete directly within the seed and multiple adults can survive, as opposed to contest strain females where only one or two adults emerge depending on the size of the seed (see also [8, 14]).

Contrary to our overall findings, previous work has demonstrated that female bruchids prefer to oviposit on larger seeds [2-4,12]. These studies presented a combination of single strains and hosts and generally utilized much larger size difference treatments than used in our experiment. A thorough study of bruchid oviposition behaviour was conducted with four strains and two hosts [11]; however, preference was not explicitly tested and seeds were

weighed after female oviposition. Results from that experiment demonstrated that contest strain females with the same origin as cultures used in our experiment had no discrimination ability when size differences between seeds were very small (e.g., 1–4%). Although experiments have been conducted with large seeds that were twice the mass of small seed [4], evidence was presented through model simulation that seed size discrimination ability may be adaptive when females are able to discriminate among numbers of eggs already laid on seeds. Therefore, females should experience stronger selection pressure to discriminate between seeds of two different sizes when there are no pristine seeds remaining [3]. Females will then choose to oviposit on seeds that have a below-average egg load [18] because competition with other larvae may result in reduced fecundity of emerging females [8]. However, we are unaware of experimental evidence demonstrating that laying eggs on larger seeds, all else being equal, will convey a fitness benefit to female *C. maculatus*. Indeed, a previous experiment using the same contest strain detected no effect of seed mass on female mass at emergence [14].

Overall, our study suggests that female *C. maculatus* have limited ability to discriminate among hosts of varying size when seed masses are not markedly different. Such fine resolution of host selection behaviour is poorly documented. Future studies should include incremental size difference treatments, which bridge the discrepancy between previous studies and that presented here, to detect whether thresholds in seed size difference exist above which females reliably choose the larger seed and/or experience fitness benefits. Possible differences among strains, which were manifested to a limited degree, also warrant further investigation. The adaptive significance of any discrimination should be tested through direct assessment of female offspring fecundity. Finally, we advocate that subtle differences in host quality should be accounted for before making assumptions regarding female discrimination ability of size alone.

Table 1: Mean (\pm standard deviation) mass (mg) of seeds from the different size class treatments

Size-difference treatment	Small	Large
<i>Mung</i>		
7%	71.96 \pm 0.39	77.14 \pm 0.73
14%	66.16 \pm 0.58	75.84 \pm 0.65
21%	64.10 \pm 0.57	79.13 \pm 0.60
<i>Adzuki</i>		
14%	197.24 \pm 2.7	224.49 \pm 3.06
28%	184.01 \pm 2.33	234.77 \pm 3.48

Table 2: Sample sizes from the different treatment combinations used to analyze potential effects of discrimination by parental mothers on body mass and fecundity of female offspring

Size-difference treatment	Small	Large
<i>Mung</i>		
7%	28	29
14%	24	28
21%	16	16
<i>Adzuki</i>		
14%	24	25
28%	23	24

Table 3: Proportion of eggs (standard error of the mean in parentheses) laid on large seeds by *C. maculatus* females presented with large and small seeds in various size-difference treatments *P* values from one-tailed *t*-tests on logit-transformed proportions; untransformed values presented for ease of interpretation. Significant deviations from the random expectation highlighted with bold. For mung replicates after 24 h, significantly higher preference for large seeds in the 21% size difference treatment than in the 7% and 14% treatments indicated with superscript letters.

Resource	Time elapsed	Size-difference treatment	Proportion of eggs on large seeds	<i>N</i>	<i>P</i>
<i>Mung</i>	12 h	7%	0.520 (0.016)	45	0.004
		14%	0.535 (0.019)	50	0.12
		21%	0.534 (0.011)	49	0.001
	24 h	7%	0.508 (0.007)	45	0.14 ^A
		14%	0.515 (0.009)	50	0.056 ^A
		21%	0.554 (0.009)	49	<0.0001^B
<i>Adzuki</i>	12 h	14%	0.500 (0.013)	50	0.11
		28%	0.487 (0.013)	49	0.84
	24 h	14%	0.514 (0.007)	50	0.032
		28%	0.516 (0.009)	49	0.043

Figure 1: Relationship between mean mung bean mass (mg) and mean (\pm SE) number of eggs laid per seed by female *C. maculatus* at 12 h (open symbols) and 24 h (filled symbols) intervals The dotted line indicates a significant relationship ($P = 0.009$, proportion of deviance explained = 0.85) at 24 h revealed by a GLM analysis.

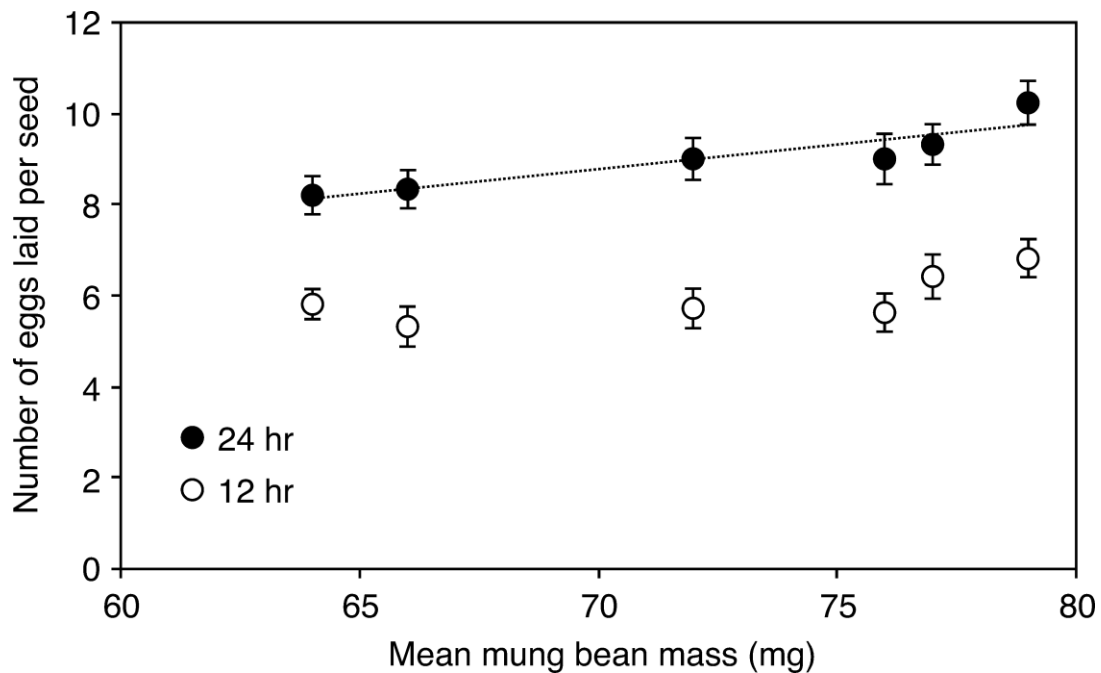


Figure 2: Relationship between mean adzuki bean mass (mg) and mean (\pm SE) number of eggs laid per seed by female *C. maculatus* at 12 h (open symbols) and 24 h (filled symbols) intervals

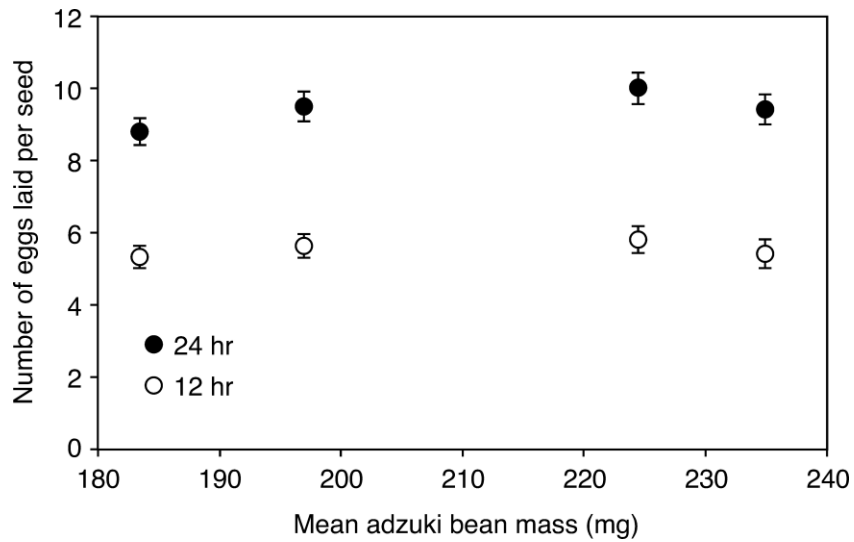


Figure 3: Mean \pm SE mass of female *C. maculatus* from offspring generation emerging from different sized (a) mung and (b) adzuki beans from size-difference treatments (large seed: filled symbols; small seed: open symbols)

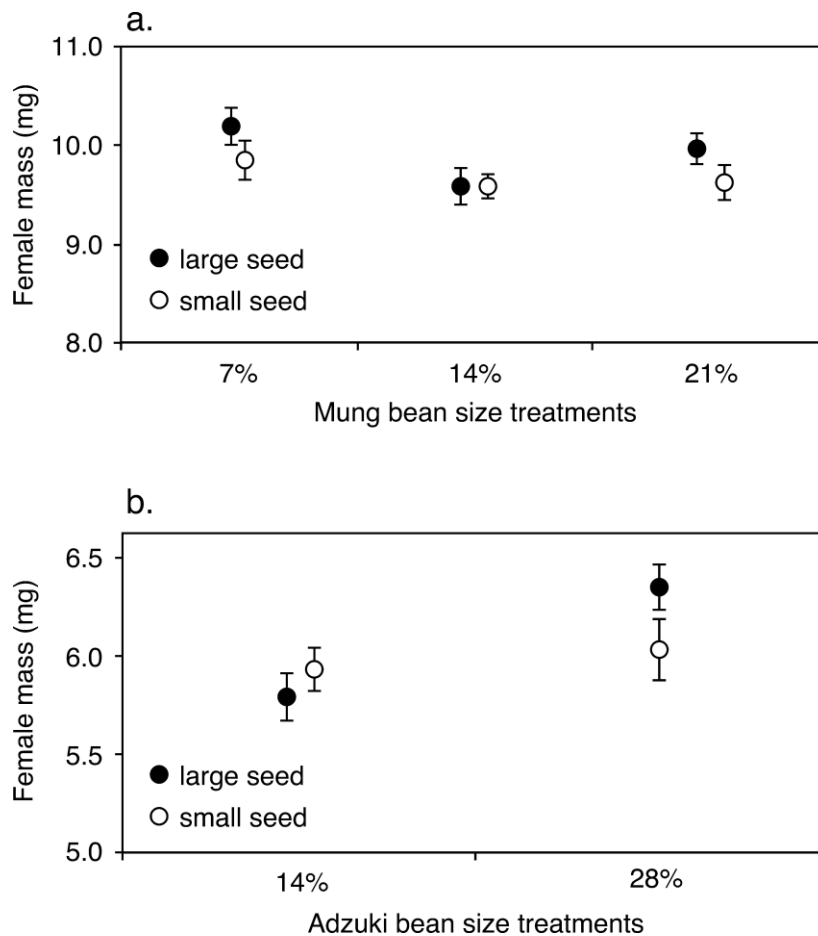
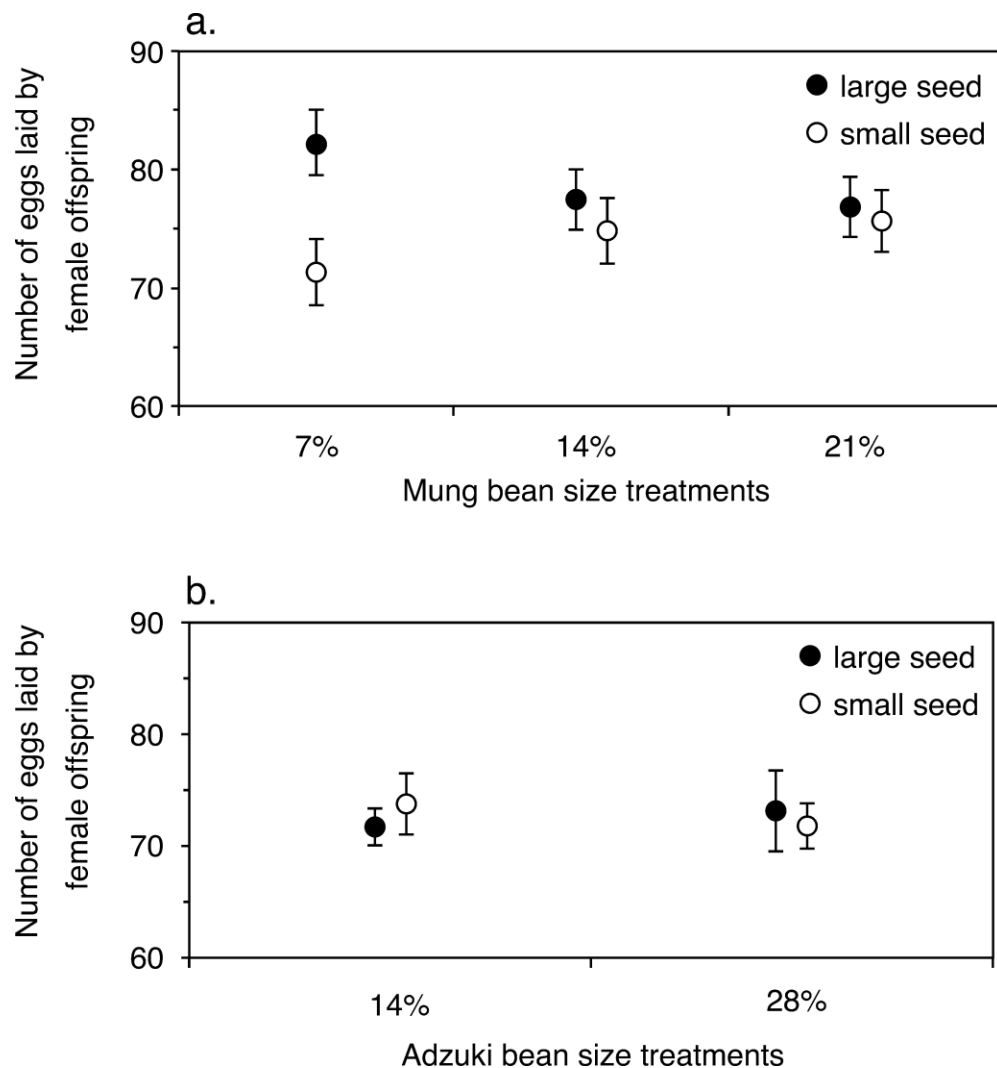


Figure 4: Mean \pm SE number of eggs laid by female *C. maculatus* emerging from different sized (a) mung and (b) adzuki beans from size-difference treatments (large seed: filled symbols; small seed: open symbols)



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