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# Variation in egg and adult production of *Callosobruchus maculatus* (F.) and *Callosobruchus chinensis* (L.) and the effect of egg density and oviposition site limitation

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## ABSTRACT

**Variation in egg and adult production in Yemen and Brazil strains of *C. maculatus* and Indonesian strain of *C. chinensis* was investigated on cowpea (*Vigna unguiculata* (L.) Walp), greengram (*Vigna radiata* (L.) Wilczek) and adzuki beans (*Phaseolus angularis* (Willd) Wight). Seed density and the host species influenced the egg and adult production of these strains to varying degrees. The decline in egg production was most notable in *C.maculatus* Yemen strain when the host seeds available for oviposition was limited. However, the egg production of Brazil strain of *C.maculatus* and the Indonesian strain of *C. chinensis* was not affected significantly by the seed size or seed density. Larvae of *C. maculatus* Yemen strain face more intense competition within the seeds due to their larger body size. Thus the females of *C. maculatus* Yemen strain tend to load eggs in relation to seed size and seed density, thereby regulating the larval competition and maximizing the individual fitness. Of the three host species, cowpea is the most suitable food substrate for adult production. The females emerged from adzuki beans were lower in body size indicating its inferiority as a food substrate.**

*Key words*: cowpea weevil, egg production, legume seeds, oviposition marker, progeny fitness.

## INTRODUCTION

The genus *Callosobruchus* constitutes six harmful species of damaging pests of stored legumes (Southgate 1964, 1965). The two most wide spread species of these beetles are the cowpea seed beetle, *Callosobruchus maculatus* (F) and the adzuki seed beetle, *Callosobruchus chinensis* (L). These two species are known to cause colossal losses to stored grain legumes in Sri Lanka (Wijeratne 1994). Life cycle of *C. maculatus* and *C. chinensis* is typically adapted to development in mature legume seeds. The larvae upon hatching, enter into the cotyledons and spend the entire larval stage within the seeds (Credland and Wright 1990). As the larvae of these beetles are unable to migrate between seeds, the oviposition behaviour of the female parent is crucial in determining the survival prospect of the progeny (Smith 1986). Recent studies have documented ample evidence to suggest that natural selection has moulded the oviposition behaviour and related life history traits such as fecundity, adult production etc. of these insects in a way that maximises the individual fitness. Evidence includes, uniform egg spacing (Messina 1989; Messina and Mitchell 1989), oviposition marker (Giga and Smith 1985; Credland and Wright 1990) and suppression of oviposition when sites are limited (Dick and Credland 1984). Suppression of oviposition reduces the larval competition because fewer eggs are laid and uniform egg spacing averages out the level of competition (Mitchell 1990).

However, these behavioral and life history traits can be highly variable within and among natural populations as a result of adaptive response to local environment (Dick and Credland 1986; Giga and Smith 1987; Messina and Mitchell 1989; Credland 1990; Messina 1990; Mitchell 1990). Knowledge on such variations will have practical relevance in developing pest management strategies to reduce losses at storage.

This study examines the variation of major life history traits of *Callocobruchus maculatus* and *Callosobruchus chinensis* with consequences for progeny fitness.

## MATERIALS AND METHODS

### Stored products

The three species of legumes used were cowpea

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(*Vigna unguiculata* (L) Walp), greengram (*Vigna radiata* (L) Wilczek) and adzuki beans (*Phaseolus angularis* (Willd) Wight). The seeds were equilibrated in controlled temperature and humidity room (CTH) maintained at 30 ± 1°C and 70 ± 5 % relative humidity for two weeks before experimental testing.

**The insects**

*Callosobruchus maculatus* (F) Brazil strain, *Callosobruchus maculatus* (F) Yemen strain and *Callosobruchus chinensis* Indonesian strain were used in the study. The insects were cultured on cowpea in the CTH room in the Department of Pure and Applied Zoology, University of Reading.

For obtaining virgin males and females, about 50 adults collected from routine cultures were introduced to glass bottles containing 125 grams of cowpea seeds. After 24 hrs the adults were separated and the seeds bearing one egg per seed were isolated in glass vials and the beetles emerged were sexed immediately using the characteristics described in detail by Southgate *et al.* (1957).

**Effect of oviposition site limitation on egg and adult production**

Five replicates of each of the three stored products were set up in Belfast-disposable plastic petridishes (ART 721) containing 10, 20, 40, 60, 80 and 100 seeds. The lid of each petri dish was perforated to enable air circulation. One virgin male and one virgin female taken within 10 hrs of emergence were placed in each petri dish and kept in the CTH room. The daily egg production was recorded until the females had ceased to lay eggs. The adult emergence was monitored daily on these treatments until 3 consecutive days had elapsed with no further emergence.

**Effect of host species on female body weight and longevity**

Adults emerged in the above experiment were sexed and then counted. The females were weighed (0.005mg) using a Cahn 2g automatic electrobalance.

The statistical computing package GENSTAT was used to carry out ANOVA.

**RESULTS**

**Egg Production**

The analysis of variance of the data on the egg production reveals that the host species had significant effect on the egg production of *C. maculatus* Yemen ($P < 0.001$) and *C. maculatus* Brazil ($P < 0.01$) strains. However, the effect was insignificant on *C. chinensis* Indonesian strain. The seed density of the three host species significantly influenced the total egg production of both strains of *C. maculatus* ($p < 0.001$). However, only the greengram seed density affected the egg production of *C. chinensis* Indonesian strain ($p < 0.001$).

**Table 1. Mean number of eggs (and SE) produced by different strains of cowpea weevil on three host species (averaged over 6 seed densities; 10, 20, 40, 60, 80 and 100 seeds per female)**

| | Host species | | |
|---|---|---|---|
| Strain | cowpea | greengram | adzuki |
| Brazil | 74.53 ± 1.51a | 77.50 ± 1.92ab | 79.87 ± 2.20b |
| Yemen | 57.30 ± 3.15a | 48.40 ± 2.66b | 62.00 ± 2.17a |
| Indonesian | 62.90 ± 2.10a | 67.30 ± 2.42 a | 69.30 ± 1.67a |

same letters in each row indicate means that are similar under a t-test (the standard errors of the difference of means are 1.78, 2.51 and 2.71 for Brazil, Yemen and Indonesian strains respectively)

**Table 2. The parameter values (and SE) for the egg production curves of *C. maculatus* Brazil, *C. maculatus* Yemen and *C. chinensis* Indonesian strains of cowpea weevil.**

**Brazil (*C. maculatus*)**

| Host species | $\beta^0$ (Asymptote) | $\beta_1$ | $r^2$ |
|---|---|---|---|
| cowpea | 77.33± 01.44 | 16.97 ± 02.26 | 99.8% |
| greengram | 80.93 ± 03.51 | 15.68 ± 04.52 | 99.8% |
| adzuki | 85.65 ± 01.52 | 11.92 ± 01.14 | 99.9% |

**Yemen (*C. maculatus*)**

| Host species | $\beta^0$ (Asymptote) | $\beta_1$ | $r^2$ |
|---|---|---|---|
| cowpea | 68.40 ± 03.21 | 06.07 ± 01.15 | 99.5% |
| greengram | 57.65 ± 04.76 | 05.88 ± 01.86 | 98.4% |
| adzuki | 66.49 ± 01.91 | 11.83 ± 01.83 | 99.8% |

**Indonesian (*C. chinensis*)**

| Host species | $\beta^0$ (Asymptote) | $\beta_1$ | $r^2$ |
|---|---|---|---|
| cowpea | 63.49 ± 02.95 | 29.34 ± 21.08 | 99.3% |
| greengram | 70.61 ± 03.64 | 14.69 ± 04.76 | 99.2% |
| adzuki | 70.63 ±02.22 | 22.69 ± 07.16 | 99.7% |

*C. maculatus* Brazil strain was more fecund on adzuki than on cowpea or greengram (Table 1). The fecundity of *C. maculatus* Yemen was lowest on greengram as compared with two other host species. The response to seed densities (oviposition sites) was clearly different between the three strains. The increase in egg production with increasing seed density was more pronounced in *C. maculatus* Yemen strain. The response of *C. chinensis* Indonesian strain was, however, indifferent to the

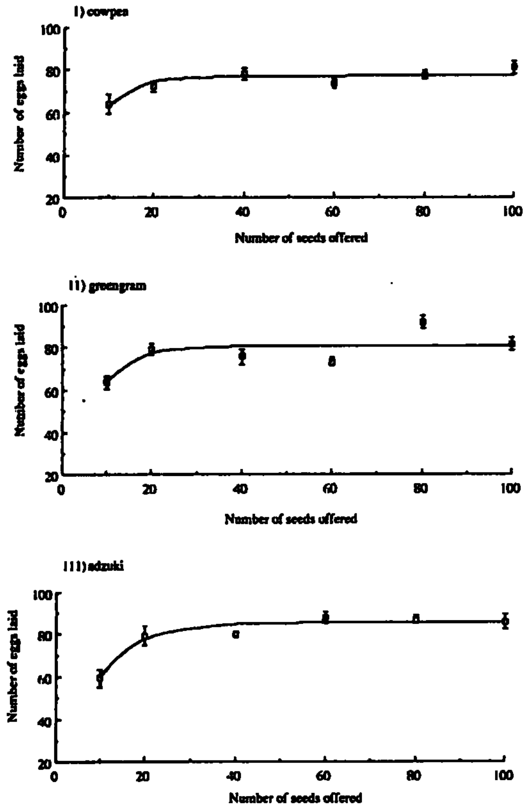


**Fig. 1 a. The egg production curve of *C. maculatus* Brazil strain on I) cowpea, II) green gram and III) adzuki. The line represents the asymptotic curve explained in the text.**

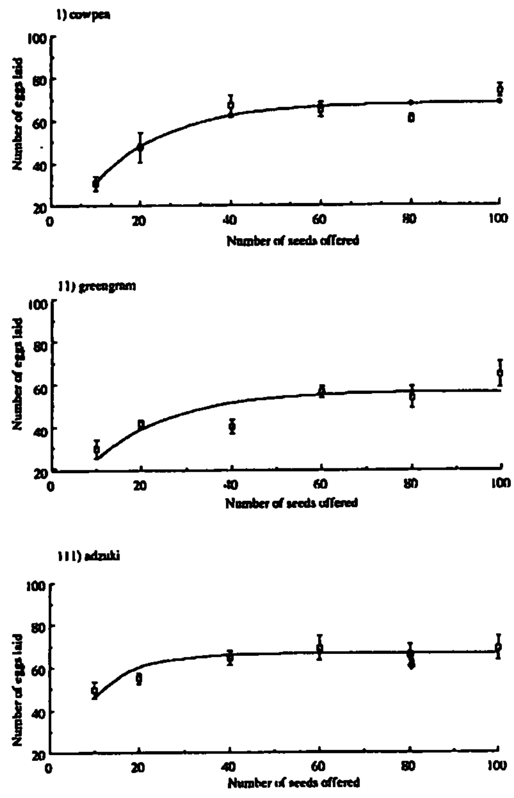


**Fig. 1 a. The egg production curve of *C. maculatus* Yemen strain on I) cowpea, II) green gram and III) adzuki. The line represents the asymptotic curve explained in the text.**

number of cowpea and adzuki seeds available for Toviposition. The relationship between egg production and the seed density can be described better by an asymptotic curve $y=\beta^0\ (1\text{-}e^{\beta_1 x})$ which represents the gradual increase of egg production to an upper limit $\beta^0$ as x (the seed density) increases (Fig. 1a, 1b & 1c). $\beta_1$ describes the rate of approach to $\beta^0$. The curves were fitted by SAS-NLIN and the values are given in the table 2. The curve describes more than 96% of the variance ($r^2$ is given in Table 2). The F values for all the curves were significant with $p<0.001$. To achieve the highest egg production *C. maculatus* Yemen strain required 40 cowpea seeds, 80 greengram seeds and 40 adzuki seeds (Fig 1a), whereas the Brazil strain required 40 cowpea seeds, 60 greengram seeds and 60 adzuki seeds (Fig 1b). *C. chinensis* Indonesian strain achieved the highest egg production on 10 cowpea and adzuki seeds which is the lowest seed density used in the experiment. However, *C. chinensis* Indonesian strain required 60 seeds of greengram to achieve highest egg production (Fig 1c).

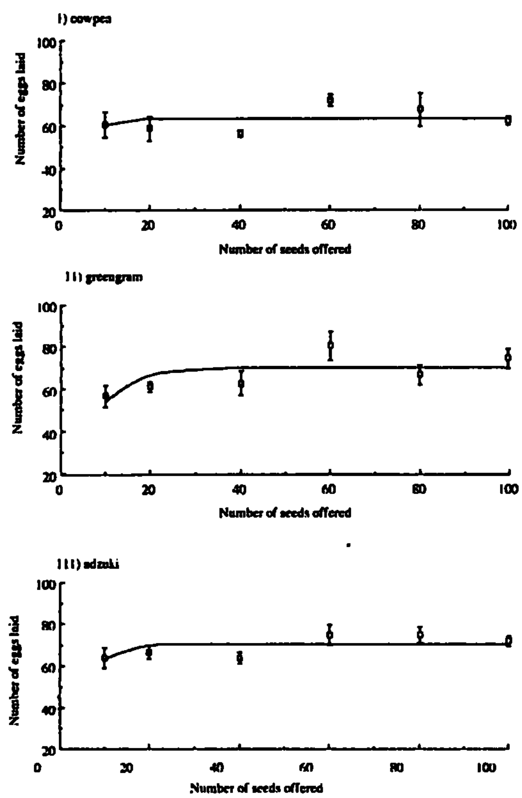


**Fig. 1 c. The egg production curve of *C. chinensis* Indonesian strain on I) cowpea, II) green gram and III) adzuki. The line represents the asymptotic curve explained in the text.**

## Adult production

The analysis of variance showed that both host species and seed density significantly influenced the adult production of the three strains ($p<0.001$).

The adult production of both strains of *C. maculatus* and the Indonesian strain of *C. chinensis* was highest on cowpea (Table 3). As in case of egg production, the relationship between the adult production and the seed density was fitted by an asymptotic curve which describes more than 98% of variance (Fig. 2a, 2b & 2c). The F values of all the curves were significant with $p<0.001$. $\beta^0$ and $\beta_1$ of *C. maculatus* values are given in Table 4. The increase in adult production of *C. maculatus* Brazil and Yemen strains are more dramatic on cowpea and greengram than on adzuki. To achieve the highest adult production, individual female of *C. maculatus* Brazil strain required 80 seeds of cowpea, 100 seeds of greengram or 80 seeds of adzuki where as *C. maculatus* Yemen strain required 100 cowpea seeds, 100 greengram seeds or 60 adzuki seeds. *C. chinensis* Indonesian strain achieved the highest adult production on 60 seeds of cowpea, 60 seeds of adzuki and 100 seeds of greengram.

**Table 3. Mean number of adults (and SE) produced on three host Species (averaged over 6 seed densities;10,20,40, 60,80 and 100 seeds per female)**

| | Host species | | |
|---|---|---|---|
| Strain | cowpea | greengram | adzuki |
| Brazil | 35.87 ± 1.96a | 20.97 ± 1.19 b | 18.70 ± 0.82 b |
| Yemen | 33.83 ± 2.80a | 26.10 ± 2.21b | 11.67 ± 0.71c |
| Indonesian | 49.30 ± 3.06a | 36.70 ± 4.29 b | 36.60 ± 3.39b |

Same letter in each row indicates means that are similar under a t-test (the standard errors of the difference of means are 1.52, 2.00 and 2.93 for Brazil, Yemen and Indonesian strains respectively)

**Table 4. The parameter values for the adult production curves of *C.maculatus* Brazil, Yemen and *C.chinensis* Indonesian strains of cowpea weevil.**

**Brazil (*C.maculatus*)**

| Host species | $\beta^0$ (Asymptote) | $\beta_1$ | $r^2$ |
|---|---|---|---|
| cowpea | 42.36 ± 05.56 | 5.84 ± 02.93 | 96.2% |
| greengram | 23.42 ± 02.45 | 08.57 ± 04.06 | 97.1% |
| adzuki | 20.26 ± 00.89 | 10.88 ± 02.43 | 99.4% |

**Yemen (*C.maculatus*)**

| Host species | $\beta^0$ (Asymptote) | $\beta_1$ | $r^2$ |
|---|---|---|---|
| cowpea | 44.19 ± 0.73 | 04.19 ± 0.22 | 99.9% |
| greengram | 47.72 ± 05.73 | 01.80 ± 00.43 | 99.5% |
| adzuki | 14.09 ± 01.06 | 05.56 ± 01.55 | 98.8% |

**Indonesian (*C.chinensis*)**

| Host species | $\beta^0$ (Asymptote) | $\beta_1$ | $r^2$ |
|---|---|---|---|
| cowpea | 58.92 ± 07.43 | 05.75 ± 02.75 | 96.6% |
| greengram | 86.13 ± 15.49 | 0.62 ± 1.15 | 95.3% |
| adzuki | 57.51 ± 16.04 | 02.46 ±01.62 | 95.5% |

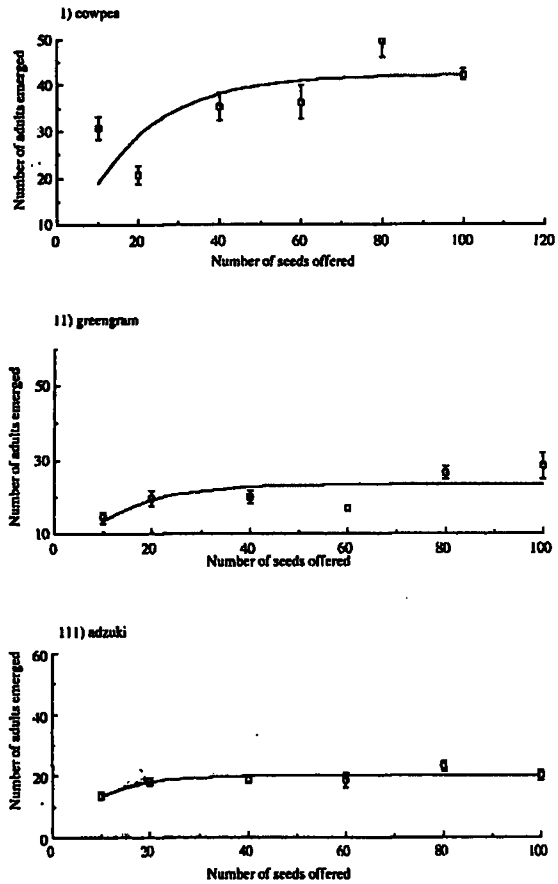


**Fig. 2 a. The adult production curve of *C. maculatus* Brazil strain on I) cowpea, II) green gram, III) adzuki. The line repre- -sents the asymptotic curve explained in the text.**

**Table 5. Mean body weight of females (and SE) at emergence on three different host species averaged over seed density**

| | *C.maculatus* | *C.maculatus* | *C.chinensis* |
|---|---|---|---|
| Host species | Brazil | Yemen | Indonesian |
| cowpea | 5.14 ± 0.024a | 6.02 ± 0.07a | 4.78 ± 0.04a |
| greengram | 5.06 ± 0.074a | 6.57 ± 0.09b | 4.69 ± 0.03a |
| adzuki | 4.28 ± 0.050b | 5.05 ± 0.05c | 4.22 ± 0.03b |

Means in each column followed by the same letter are not signific- -antly different at 5% level (t test).Tthe standard error of difference of means is 0.073.

## Effect of legume species on female body weight

The analysis of variance shows that the host species significantly influenced the body weight of the females. Table 5 shows that the females emerged from adzuki are significantly smaller and lower in body weight. *C. maculatus* Yemen females emerged from greengram are slightly higher in body weight.

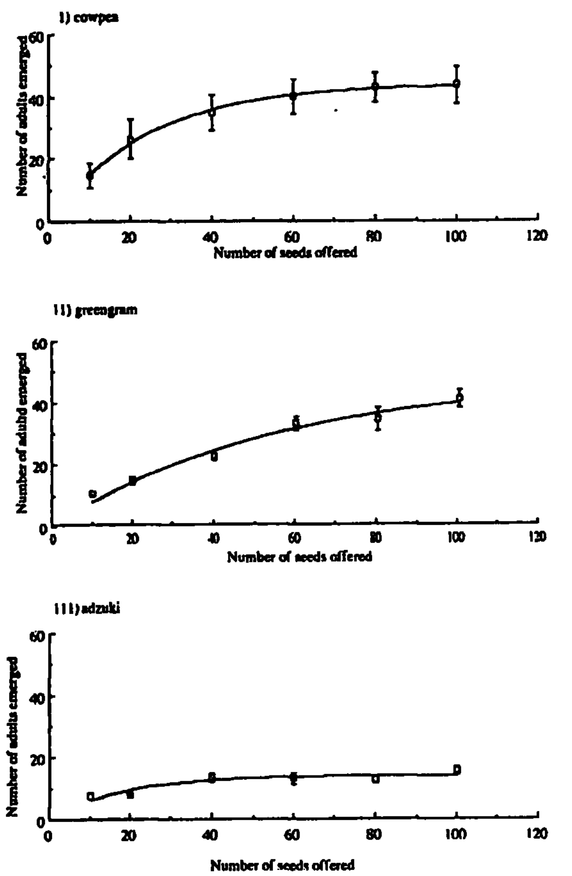


Fig. 2 b. The adult production curve of *C. maculatus* Yemen strain on I) cowpea, II) green gram, III) adzuki. The line represents the asymptotic curve explained in the text.

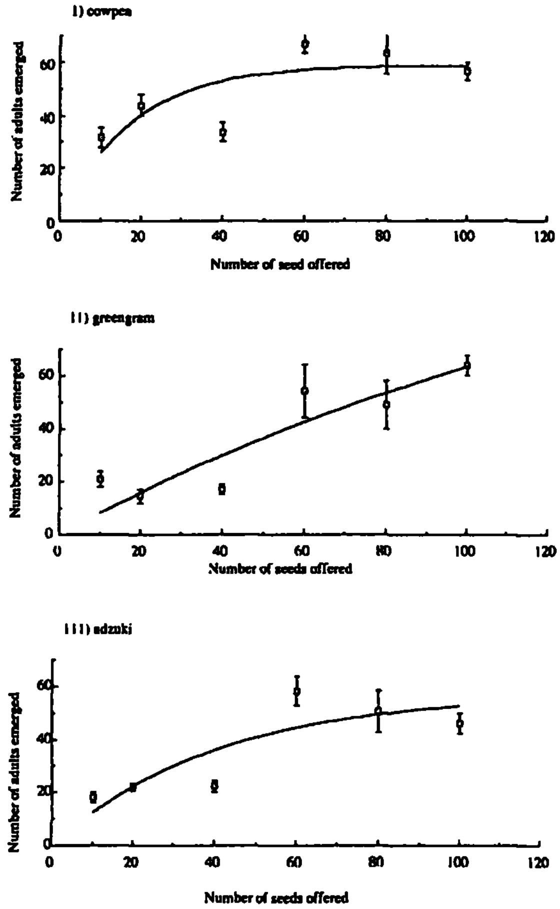


Fig. 2 c. The adult production curve of *C. chinensis* Indonesian strain on I) cowpea, II) green gram, III) adzuki. The line represents the asymptotic curve explained in the text.

## DISCUSSION

The experiments revealed the interspecific and intraspecific variation of behavioural traits and some major life history traits of *C. maculatus* Brazil, *C. maculatus* Yemen and *C. chinensis* Indonesian strains. There was a clear variation of the oviposition response of these strains to the seed density and the host species. Oviposition behaviour is a catenary process which is governed by a large number of factors. Many workers have agreed that the egg density on the seed and the seed size takes precedence over the other factors in identifying the kind of hosts in releasing eggs. The decline in egg production was most notable when the females of *C. maculatus* Yemen were restricted to a fewer number of greengram seeds. On the whole, the response to seed density (oviposition site) was more apparent in *C. maculatus* Yemen strain than in *C. maculatus* Brazil strain. It was less conspicuous in *C. chinensis* Indonesian strain. The effect of host species on the egg production of *C. maculatus* Yemen strain was largely due to its seed size. As the larval competition within the seed is a major functional determinant of the life history traits of these insects, the oviposition behaviour has been moulded to load eggs in relation to seed size and the seed densities, thereby regulating the larval competition and maximizing individual fitness. The females of *Callosobruchus* species possess the ability to recognize the eggs already available on the seeds and space the eggs uniformly on the resources. This is mainly achieved by a chemical secreted at the time of oviposition (Utida 1943; Avidov *et al.* 1965; Mitchell 1975; Oshima *et al.* 1973). The response to this chemical varies among strains and the species (Messina and Renwick 1989). Dick and Credland (1984) studied the variation of this trait among the strains of *C. maculatus* and concluded that the seed density had greater effect on the egg production of Yemen strain. They attributed this ability of Yemen strain to produce most effective chemical and respond strongly not only to its own chemical but also to the chemicals secreted by other strains. Thus, it can be stated that the egg production of the strains that respond strongly to this chemical is affected more by the oviposition site limitation and the seed size.

The inhibition of oviposition on seeds with a load of eggs clearly limit the competition that the larvae face. from older larvae that emerged from eggs already present on seeds (Mitchell 1990). Since progeny fitness declines monotonically with increasing larval density, high degree of inhibition of egg production on fewer seeds is expected (Mitchell 1975: Smith and Lessells 1985). Perhaps the high level of egg production with less response to seed density by *C. maculatus* Brazil strain and *C. chinensis* Indonesian strain may represent adaptation to adult crowding acquired through the past environment.

With regard to adult production, the increase in percentage of emergence with seed density in *C. maculatus* in cowpea and greengram is more dramatic than in adzuki. Percentage emergence of all 3 strains was highest on cowpea, indicating that cowpea offers the most suitable substrate for adult production. The low adult production in adzuki and low body weight of the resulting females indicate its inferiority as a food substrate for larval development.

Dick and Credland (1984) showed that the competition among the larvae of *C. maculatus* Yemen strain is more intense than that among the larvae of IITA and Compinas strains due to their larger body weight. This intense competition among larvae within the seeds results in higher larval mortality and lower percentage of adult emergence (Campinas refers to Brazil strain in this experiment). However, in our experiment, the total adult production of the two strains of *C. maculatus* appears to be same on cowpea (Table 3). This may be because of the influence of high seed densities on the overall means. As compared with the *C. maculatus*, Brazil and Yemen strains, the adult emergence of *C. chinensis* Indonesian strain was always higher on the 3 species of host seeds indicating less intense larval competition within the seed in the latter case. This may be due to the smaller body size of *C. chinensis* Indonesian strain (Table 5).

The relationship between the seed density and the adult production on different host species is of considerable importance in explaining the population build up in stored legumes. Variation of behavioural and life history traits among populations poses potential problems in pest management systems. The major obstacles posed by these variations is that the control strategies developed in a single area may not be equally successful in other areas in ensuring good control. Therefore, such variations of ecologically important characters have to be adquately studied before developing pest management strategies for the control of these insects under storage conditions. Another aspect which is important but was not investigated here is the effect of seed density on the production of winged form adults. It has been demonstrated that when the food supplies in the stores are exhausted, the populations of *C. maculatus* trigger off dispersal with the production of winged adults which could initiate actual infestation in the field (Barrer 1983; Messina and Renwick 1985). If the specific mechanism of the production of the winged adults is understood, initiation of pest infestation in the field can be checked, leading to more successful control of the pest under storage condition.

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