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Response of the Seed Beetle, *Callosobruchus maculatus* (F) to Differences in Seed Size in a Variety of Cowpea, *Vigna unguiculata* (L) Walp.

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ABSTRACT

This study investigated selective oviposition behaviour of the seed beetle, *Callosobruchus maculatus* (F.) originating from Borno (Nigeria), Burkina Faso and Sierra Leone when provided with cowpea, *Vigna unguiculata* (L.) Walp. (California black-eyed variety) seeds of different sizes. Oviposition preference and effects of variation in seed size on food consumption, development, reproduction and survival of the beetles were determined. Females of the three beetle populations always laid more eggs on the large seeds. More eggs were also laid on the medium seeds than on the small seeds. For each beetle population, seed size did not influence development time. Larvae generally consumed more food from large seeds and yielded heavier females which were more fecund. Larvae of beetles from Burkina Faso were generally more voracious. Significantly, more adults emerged from the large seeds than from the small seeds, following an initial density of 10 or more hatched eggs per seed. The results are discussed in relation to previously published reports.

INTRODUCTION

The seed beetle, *Callosobruchus maculatus* (F.) infests seeds of numerous species of wild and cultivated legumes, especially species in the genus *Vigna* (Southgate, 1978). *C. maculatus* causes very serious damage to stored cowpeas, *V. unguiculata* (L.) Walpers, an important dietary staple in many parts of the tropics and sub-tropics. Adaptations for exploiting stored cowpeas by *C. maculatus* probably began to evolve with the domestication of the crop about 6000 years ago (Ng. & Marichal, 1985). The beetle's life cycle is relatively simple in the storage environment. Females deposit eggs singly on the surface of cowpea seeds. On hatching, the larvae penetrate the testa and remain in the seed until development is complete. Adults mate and reproduce within hours after emergence, and typically live for a few to several days depending on ambient temperature. They require neither food nor water for reproduction, and typically do not obtain either in the storage environment. Oviposition decisions made by the females are the critical determinants in the life cycle because they set the conditions in which an offspring must develop from egg to adult (Mitchell, 1975).

The behavioural repertoire during oviposition in *C. maculatus* has been observed and analysed (Wasserman, 1985; Wilson, 1988, Ofuya & Agele, 1989; Thantianga and Mitchell, 1990; Messina & Dickinson, 1993; Parr, 1994).

Females prefer egg-free seeds over egg-laden seeds, and also distinguish seeds bearing different numbers of eggs and developing larvae, during oviposition (Messina & Renwick, 1985; Wilson, 1988; Ofuya, 1989). Ovipositing females also seem to respond to several other aspects of a seed; the species of seed, its size, whether it is cracked, and the number of adult emergence holes it bears (Mitchell, 1983; Ofuya & Agele, 1990; Thantianga & Mitchell, 1990).

Discriminatory oviposition behaviour in many phytophagous insects may have evolved as an adaptation for reducing the probability of intraspecific and interspecific competition and ensuring higher progeny survival (Prokopy *et al.*, 1984). Many strains of *C. maculatus* have been reported to show preference for large seeds during oviposition (Mitchell, 1990). This presumably ameliorates the intensity of larval competition such that larvae compete in a seed with a larger than average quantity of food. Selection of larger seeds for oviposition would clearly be adaptive if the number of survivors from a seed increases with seed size, but this has not been

examined (Mitchell, 1990). Grain size has been observed to influence oviposition, distribution of eggs and adult emergence of *Sitophilus granarius* L. (Stejskal and Kucerova, 1996). This paper reports an investigation into selective oviposition behaviour of three West African strains of *C. maculatus* in terms of seed size preference using California black-eyed cowpea, a known susceptible variety. The effects of variation in seed size on food consumption, development, reproduction and survival of the beetle are considered.

MATERIALS AND METHODS

Beetle populations: *C. maculatus* originating from Nigeria, Burkina Faso and Sierra Leone were used. The cultures were maintained and the study conducted at 27 ± 1 C and $70 \pm 10\%$ relative humidity in a controlled temperature and humidity (CTH) room using culturing procedures described by Dick & Credland (1984).

Cowpea variety:

The variety used was California black-eyed cowpea supplied by Helm Bean & Seed Warehouse Inc. Helm, California 93727, USA. The seeds were first deep frozen for 10 days to kill off any prior infestations and were then conditioned for two weeks in a controlled temperature and humidity room at 27 ± 1 C and 70% relative humidity.

Effect of seed size choice for oviposition:

Conditioned cowpea seeds were weighed individually and grouped into small (<150 mg), medium (200 - 250 mg) and large (> 280 mg). Sixty seeds consisting of 20 from each group, were then mixed in a plastic Petri plate (8.5 cm diameter) and infested with a freshly emerged and mated pair of adults. After 24 hours, the adults were carefully removed and eggs laid on seeds belonging to each size group were counted. The insects were then returned onto the seeds. The number of eggs laid on the seeds were also counted at the death of the female.

This procedure was carried out for each strain of *C. maculatus* in twenty replications.

Effect of seed size on food consumption development and fecundity:

Conditioned small, medium and large cowpea seeds were used. For each beetle strain, 100 seeds of each size group were put into a crystallising dish and infested with newly emerged adults (30 females and 30 males), for about 14 hours. Time of egg laying was recorded. Excess eggs were thereafter removed

from the seeds so that each seed bore one egg and the seed was weighed. Such seeds were placed in plastic replidishes (10 X 10 cm) for adult emergence. In the replidishes each seed occupied a separate compartment. The replidishes were fitted with lids which prevented change of compartment by emerging adults. Time of adult emergence from each seed was noted. The final weight of the seed from which an adult emerged was also recorded. The weight of the emerged adult was taken using a Sartorius 4501 micro balance accurate to 0.001 mg. Twenty pairs emerging from each size group were mated and each placed onto 40 sieved and conditioned cowpeas inside glass tubes. The number of eggs laid were counted after the death of the female.

Effects of seed size on survival:

Only the Borno and Sierra Leone strains were used. For each strain, 20 seeds of each size group were made to bear six, ten, sixteen and twenty eggs per seed, respectively, over a 24 hr period of oviposition by many newly emerged mated pairs of adults. Since all eggs may not hatch, only seeds that bore hatched eggs ascertained about 10 days after oviposition, were used. They were placed in replidishes, as described previously, for adult emergence. Adult insects were counted and removed as they emerged from the seeds over a two week period.

Experimental design and data analysis:

The experiment always involved two factors, either three bruchid populations and three seed sizes or three seed sizes and four initial larval densities. Data were, therefore, subjected to two-factor analyses of variance. Percentage data were arcsine transformed before analysis. The LSD statistic was used to separate significant means.

RESULTS

Effect of seed size on seed choice for oviposition:

In all three populations of *C. maculatus*, the number of eggs deposited on the large seeds by the female beetles in 24 hrs was significantly greater ($P < 0.05$) than the number laid on medium and small seeds (Table, 1). The number of eggs laid on the medium seeds was also significantly more than the number laid on the small seeds.

During this period, the number of eggs laid by the beetle populations for each seed size was not significantly different ($P>0.05$).

Effect of seed size on food consumption, development and fecundity:

The development period of each of the three beetle populations was not significantly different ($P>0.05$) in the differently sized cowpea seeds (Table, 2). For the populations from Burkina Faso and Sierra Leone, seed weight loss caused by one larva was significantly higher ($P<0.05$) in large and medium seeds than in small seeds for emerged females (Table, 3). For the Borno population, weight loss due to one larva was not significantly different ($P>0.05$) between the seed sizes for emerged females. Irrespective of seed size, weight loss caused by Burkina Faso adults was significantly higher than loss caused by Sierra Leone adults.

TABLE 1. The mean (\pm SE) number of eggs laid in 24 hr. on Differently sized California Black-eyed cowpea seeds by Females of Three Populations of *C. maculatus* (CM).

Seed Size	Mean (\pm SE) number of eggs laid by:		
	Burkina Faso CM	Nigeria CM	Sierra Leone CM
Small	2.3 \pm 0.08	1.8 \pm 0.06	2.1 \pm 0.04
Medium	7.4 \pm 0.62	5.3 \pm 0.41	8.2 \pm 1.02
Large	14.6 \pm 1.23	12.7 \pm 0.89	6.3 \pm 2.11
LSD _{0.05} = 4.23			

TABLE 2: The mean (\pm SE) Developmental Period (days) of Three Populations of *C. maculatus* in seeds of California black-eyed Cowpea of Different sizes.

Seed Size	Beetle population		
	Burkina Faso	Nigeria(Borno)	Sierra Leone
Small	25.0 \pm 0.18	25.1 \pm 0.31	25.0 \pm 0.14
Medium	25.1 \pm 0.21	24.9 \pm 0.22	25.2 \pm 0.16
Large	25.2 \pm 0.14	24.6 \pm 0.26	25.8 \pm 0.24

TABLE 3 : The mean (\pm SE) Seed Weight loss (mg) Caused by one Larva of Three Populations of *C. maculatus* Developing alone in Single Seeds of California black-eyed Cowpea of Different Sizes.

Seed size	Bruchid population		
	Burkina Faso	Nigeria	Sierra Leone
Small	19.1 \pm 0.41	18.7 \pm 0.42	15.6 \pm 0.64
Medium	23.6 \pm 0.61	19.7 \pm 0.51	18.8 \pm 0.46
Large	24.5 \pm 0.83	20.1 \pm 0.63	19.6 \pm 0.81
LSD _{0.05}	= 3.10		

In all three populations, bigger females emerged in the large and medium seeds than in the small seeds (Table, 4). For each seed size, the weight of adults of the beetle populations was similar. Table 5 shows the mean number of eggs laid by single mated females of the three beetle strains reared individually in the differently sized cowpea seeds. Females reared from the large and medium seeds were significantly ($P < 0.05$) more fecund than females produced from small seeds. For each seed size females of the beetle populations were similar in fecundity.

Effect of seed size on survival:

For the Borno strain, the differently sized cowpea seeds produced the same number of adults when each seed initially bore six hatched eggs (Table, 6). Significantly ($P < 0.05$) more adults emerged from the large seeds than from the small seeds when each seed initially bore 10 or more hatched eggs. Irrespective of seed size, percentage adult emergence was significantly higher at initial larval densities of 6 and 10 than at 16 and 20. A similar trend was observed for the Sierra Leone beetles (Table, 7).

TABLE 4: The mean (\pm SE) Adult Weight (mg) at Emergence of Three Populations of *C. maculatus* obtained from Seeds of California black-eyed Cowpea of Different Sizes.

Seed size	Bruchid population		
	Burkina Faso	Nigeria	Sierra Leone
Small	6.6 \pm 0.61	6.0 \pm 0.14	6.1 \pm 0.21
Medium	8.1 \pm 0.17	7.7 \pm 0.11	7.8 \pm 0.20
Large	8.2 \pm 0.15	7.8 \pm 0.19	7.7 \pm 0.19
LSD _{0.05}	= 0.63		

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TABLE 5: The mean (\pm SE) Number of Eggs laid by Single Mated Females of Three Populations of *C. maculatus* Reared Individually in Different Sized California black-eyed Cowpea Seeds.

Seed size	Bruchid population		
	Burkina Faso	Nigeria	Sierra Leone
Small	110.2 \pm 5.34	104.7 \pm 5.81	106.8 \pm 5.78
Medium	135 \pm 4.61	123.5 \pm 4.89	132.8 \pm 6.41
Large	141 \pm 4.03	126.4 \pm 6.21	131.1 \pm 5.46
LSD _{0.05} = 16.27			

TABLE 6. The mean (\pm SE) percentage adult emergence of the Borno population of *C. maculatus* from differently sized California black-eyed cowpea seeds initially bearing 5, 10, 16 and 20 hatched eggs respectively.

Seed size	Mean % adult emergence			
	Initial larval density in seed:			
	Six	Ten	Sixteen	Twenty
Small	75.0 \pm 1.19	70.0 \pm 1.21	38.8 \pm 1.80	32.0 \pm 2.20
Medium	80.0 \pm 2.29	81.0 \pm 1.30	49.4 \pm 2.20	34.5 \pm 2.60
Large	85.0 \pm 3.20	86.0 \pm 2.10	65.5 \pm 2.30	61.0 \pm 2.10
LSD _{0.05} = 9.05				

TABLE 7. The mean (\pm SE) percentage adult emergence of the Sierra Leone population of *C. maculatus* from differently sized California black-eyed cowpea seeds initially bearing 6, 10, 16 and 20 hatched eggs respectively.

Seed size	Mean % adult emergence			
	Initial larval density in seed:			
	Six	Ten	Sixteen	Twenty
Small	75.0 \pm 1.60	63.0 \pm 2.10	31.9 \pm 1.90	22.0 \pm 1.40
Medium	81.7 \pm 1.80	76.0 \pm 1.90	50.6 \pm 2.40	27.0 \pm 3.40
Large	81.7 \pm 2.20	85.0 \pm 2.70	58.1 \pm 3.30	53.0 \pm 3.10
LSD _{0.05} = 10.28				

DISCUSSION

Inter- and intra- varietal differences in seed characteristics including seed size is common among cowpea varieties (Young, 1985). Many of these seed characteristics are known to influence seed selection for oviposition by females of *C. maculatus* in the storage environment. Females of many beetle strains discriminate between the size of host seeds while others do not (Mitchell, 1990). The three populations used in this study clearly preferred the large cowpea seeds for oviposition. Many elucidations can be given for this behaviour. Thanthianga & Mitchell (1990) suggested that larger seeds are more likely to be encountered during the random movements by ovipositing females. The larger cheek area, the most favoured seed part for oviposition (Ofuya, 1987), will allow much heavier egg load on large seeds. The influence of some previously laid eggs in reducing further oviposition (Messina & Renwick, 1985), may be more easily obscured (Ofuya & Adenekan, unpublished) in large than in small seeds. Berg & Mitchell (1993) reported that strains of *C. maculatus* that disperse eggs at random tend to lay eggs on the largest available seeds first, while strains that uniformly disperse eggs do not respond to host size when ovipositing. Egg dispersion by females of the populations used in this study was not determined, but data obtained for some beetle strains from West Africa seem to suggest egg dispersion in some intermediate fashion between random and uniform distributions (Mitchell, 1990; Messina, 1993).

It has previously been shown that the number of adult *C. maculatus* which can emerge from single legume seeds is dependent not only on the number of eggs initially present but also the strain or biotype under investigation (Dick & Credland, 1984; Credland, 1986), as well as the kind of legume (Mitchell, 1990). Intra-varietal differences in seed size has been shown here to be an additional factor which significantly influences larval survival in *C. maculatus*. Preference for larger seeds for oviposition by the Nigeria (Borno) and Sierra Leone populations is clearly adaptive because the number of survivors from a seed generally increased with seed size. Preferential oviposition on large seeds, therefore, unequivocally ameliorated the intensity of larval competition. When the females were forced to oviposit on seeds already carrying eggs, they selected the largest seeds so that their larvae competed in a seed with a larger quantity of food, and more larvae successfully metamorphosed to adulthood. The adult emergence data following the different initial larval densities reveals that the kind of larval competitive behaviour was not modulated in response to seed size. In all the differently sized seeds, number of bruchids surviving to adulthood significantly decreased increased with increase in initial larval density from 6 and 10 larvae. The observed larval behaviour in the seeds is consistent with scramble competition (Smith & Lessells, 1985; Smith, 1990; Toquenaga, 1993). Larval competitiveness can be modulated in response to seed size, perhaps presumably at

lower initial larval densities (e.g. Toquenaga, 1993) than used in this study. Credland & Dick (1987) also argued that the competition between larvae of *C. maculatus* in a cowpea seed will always lead to a scramble type of outcome, but that the larval densities required to demonstrate that result may vary from one strain to another. Preferential selection of larger seeds for oviposition is further advantageous in relation to fitness in female beetles. It increases fitness on the basis of lifetime offspring production (Koztowski, 1993) which is greater in females reared on larger seeds. It is not surprising to have recorded the general synchrony of larger food intake in large seeds producing larger females with higher fecundity. *C. maculatus* is already known to exhibit a strong relationship between larval competition, adult weight at emergence and fecundity (Smith & Lessells, 1985; Credland et al., 1986; Messina, 1991a; Colgrave, 1993). However, since one larva infested each seed in the assessment of growth and development of the beetle in this study, it could easily have been assumed that the food resources provided with each seed size was sufficient for the full expression of the growth, development and reproductive potential of each beetle type under the experimental conditions. It is known that females of some strains of *C. maculatus* exhibit a kind of 'numerical response' by increasing egg laying with increasing seed population up to a point (Credland, 1986; Ofuya, 1987). It is probable that for some strains, larvae which produce adult females may exhibit a 'functional response' by increasing food intake when food resources are plentiful. This merits empirical verification with several other *C. maculatus* populations. It is conceivable that larvae of strains which do not respond to seed size or eliminate competitors such that only one adult is produced per seed (Mitchell, 1990; Messina, 1991b; Mitchell, 1990; Messina and Dickinson, 1993; Ofuya and Credland, 1995). The larvae of the beetle from Burkina Faso was more voracious in this study. This was, however, not translated in terms of weight and fecundity of its female and is consistent with the conclusion of Colegrave (1994) that there is no effect of larval competition on adult fecundity independent of its effect on adult weight. Overall, seed size appears to be a major selective factor affecting life-history traits in *C. maculatus* populations. Theoretical and empirical studies have suggested that long-term association with a relatively small-seeded host may promote stronger competitive interactions among larvae and perhaps also greater avoidance of occupied seeds by ovipositing females (Smith and Lessells, 1985; Messina, 1991a; Toquenaga & Fujii, 1991; Toquenaga, 1993). Empirical evidence has been provided in this study to show that intra-varietal differences in seed size which characterise cowpeas may also modulate larval competition and female fitness in the beetle. Bionomic variation in *C. maculatus* populations was supported by the observed differences in the voracity of larvae of the beetles used.

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