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THE EVOLUTION OF OVIPOSITION TACTICS IN THE BEAN WEEVIL, *CALLOSBRUCHUS MACULATUS* (F.)¹

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Abstract. A sizeable fraction (7%–17%) of the mung beans that are the preferred food of *Callosobruchus maculatus* are not large enough to support two larvae. Whenever two or more eggs are on a bean, development takes 40 days rather than 33 days, and only 8% of the second eggs develop even in beans with resources enough for two larvae. This larval competition confers an advantage on females that disperse eggs uniformly. Females tend to avoid adding second eggs as long as there are unused beans. Survivorship of single eggs on beans increases with weight ($l_1 = .005 \text{ mg} + .368$) and females oviposit on the largest of the unused beans first. Survivorship of the second egg ($l_2 = .31$), due principally to mortality of the first egg, is about half that of the first egg; a second or third egg is added after nearly all the beans carry one or two eggs respectively.

With these constraints the beetle may maximize fitness if it knows the weights and egg loads of all available beans. The actual performance falls short of achieving maximum fitness and the oviposition of the beetle fits a computer simulation that makes decisions after comparing the weight and egg load of the present bean with the last bean encountered. The performance of the beetle can be appropriately evaluated against models for unspecialized beetles that oviposit randomly and for beetles with maximum fitness. This shows that the beetle gains about 70% of the fitness that it could evolve.

Key words: Bean weevils; *Callosobruchus maculatus*; evolution; oviposition tactics.

INTRODUCTION

The larvae of many bruchid beetles can make no choices. They must feed, grow, and mature in a bean that was selected for them by their mother. If the survival of the larvae is differentially affected by the size and quality of the beans, selective pressures will favor females that discriminate among beans and avoid overloading a bean.

These beetles are known to be selective in the kind and size of bean on which they place eggs (Avidov et al. 1965a, b; Booker 1967, Jakhmola and Singh 1971). They spread their eggs uniformly over a set of beans (Utida 1943), and one species, *Callosobruchus chinensis*, inhibits second ovipositions through a chemical marker (Oshima et al. 1973). None of these authors have gone beyond descriptions of behavioral phenomena in order to ask how the beetles might benefit from their oviposition behavior. Most of the previous observations are supported and extended in this paper. An analysis of the fates of eggs on beans of different sizes and at different densities is used to define the selective pressures in the system for the bean weevil, *Callosobruchus maculatus* (F.).

All feeding is done during the larval stage; the adults of *C. maculatus* require neither food nor water after emergence. The adults only mate and oviposit; thus, *C. maculatus* is an ideal subject for studying

oviposition behavior independent of other phenomena.

The following questions will be considered: (1) Are all beans equally satisfactory sites for larval development? (2) How does the density of eggs on beans affect survivorship? (3) Does a specialized pattern of oviposition increase the fitness relative to that expected with a random dispersion of eggs? The sequence of questions logically defines the causes (1, 2) that could result in the evolution of specialized oviposition behavior (3). In practice it is most efficient to see if a nonrandom oviposition behavior has evolved and then to identify the components of fitness. This study defines the oviposition tactics and then develops independent measures of the selective forces driving the system.

MATERIALS AND METHODS

The stock culture was obtained from and maintained on mung beans (*Phaseolus aureus*) purchased in Columbus, Ohio. All culturing and experiments were done in a laboratory regimen resembling conditions under which the beetle has flourished as a pest for hundreds of years. It is known that the maximum response of *Callosobruchus* to the variations in temperature (20°–23°C) and the consistently low humidity of the laboratory would not measurably affect any of the experiments (Schoof 1941, Booker 1967). The frequency of the dispersal morph (Utida 1972) was extremely low in the cultures, and all experiments involved only the smaller sedentary phase of *C. maculatus*.

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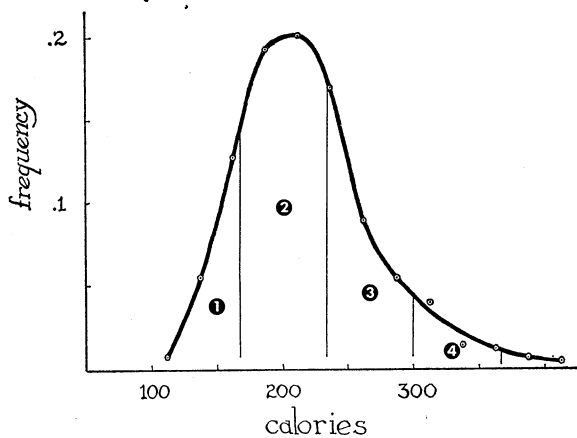


FIG. 1. Frequency distribution for the population of beans from which beans were drawn for oviposition experiments (Fig. 2). Vertical lines separate size classes of beans; numbers in circles specify the maximum number of ♀♀ that could develop on a bean of the indicated size range.

LIFE HISTORY

Females lay eggs individually on beans, and the eggs are protected by a thin hard covering. After 8–10 days development, the larva hatches out and chews into the bean. Because the larva does not move from bean to bean, it must complete development in the bean selected by its mother. Development from egg to adult takes 33.6 ± 0.6 days ($n = 131$) and there are no significant differences in the developmental time of the two sexes. Newly emerged adult females have a dry weight of $2.07 \pm .05$ mg ($n = 25$) and carry 84.6 ± 4.2 eggs ($n = 9$) that make up about 1.08 mg of her weight. Males weigh $1.23 \pm .03$ mg ($n = 28$). Males live about 10 days, females about 12 days.

If some beans are small in terms of the needs of a larva, then prudence in oviposition can save some larvae from hatching out on a bean too small to support the load of eggs. It is therefore necessary to know the dimensions of beans and how much a beetle larva eats in order to determine if bean size may impose limits to oviposition patterns.

RESOURCE RELATIONS

I determined the quantity of bean consumed by a larva by weighing a bean before the larva began to feed and then weighing what was left after the adult emerged. These values were converted to dry weight equivalents with coefficients from uninfected controls treated the same way as the experimental beans. Females eat 14.5 ± 0.4 mg ($n = 25$) dry wt of bean and males eat 9.5 ± 0.3 mg ($n = 28$). The caloric equivalents for beetles and beans are 7.21 ± 0.11 Cal/mg ($n = 4$) for females and 6.99 ± 0.08 Cal/

mg ($n = 4$) for males. The beans yielded 4.45 ± 0.13 Cal/mg ($n = 5$). Hence, females eat 64.5 Cal of bean and convert that into a 14.9-Cal beetle. Their gross efficiency is 23%; that of males is 20%.

An estimate of the minimum-sized bean required for the development of a given load of eggs must include an estimate of how much of the bean must be left in order to provide a husk for the protection of the pupa. Husk size was estimated from a set of beans exploited by a dense population of beetles for a period in excess of three generations. A non-overlapping sequence of larvae exploited the beans, and most of the beans had dead larvae in them, suggesting that the husks were inadequate protection for the larvae. Twenty husks had a mean weight of 24.1 ± 1.52 mg and the minimum husk size in the sample was 9 mg (40 Cal). The minimum value will be used and is a conservative estimate for husk size.

At the very least, then, a single female requires a bean with $65 + 40$ Cal, two females will require $130 + 40$ Cal, etc. The distribution of beans by caloric content (Fig. 1) shows that 17% of the beans have fewer calories than needed by two females. Two males will require 125 Cal, and only 0.8% of the beans would be inadequate for two males. The average mortality for two eggs can be specified as the mean for the binomial expansion with the sexes equal (as is true for *C. maculatus*), which is 7%, or it might be argued that the reduction of males is unimportant and that mean female losses, 15%, is the appropriate value. In either case, simple resource limits would produce sufficient mortality to give a selective advantage to beetles that avoid having more than one larvae feed in a bean.

With random oviposition, any larva that senses a second larva in its bean would gain 7%–17% survivorship by excluding the other larva. The evidence for such larval competition is clear. When there is one egg on a bean, development takes 33.6 ± 0.6 days ($n = 131$); when there are two eggs per bean it takes 40.1 ± 0.4 days ($n = 228$); and for three eggs per bean it takes 45.1 ± 0.7 days ($n = 89$). At least 83% of the beans should have the resources necessary for the development of two eggs, but only 8% of the beans with two eggs on them did have a second beetle emerge. These data are from a set of beans that had been exposed to beetles for 4 h, so the age of the eggs differed by less than 4 h.

It is obvious that an interaction between the larvae slows down the development of larvae when more than one egg is present. Resource relations could account for the evolution of larval interactions but they will not explain why the survivorship of the second and third beetle is less than one-tenth of the survivorship expected from simple resource relations.

TABLE 1. The sum of the distributions of eggs by nine isolated *C. maculatus* ♀♀ presented with a surplus of beans. Every ♀ departed from the Poisson in the same pattern at significance levels $< .001$; hence the data are pooled

	Eggs per bean		
	0	1	2
Observed	664	696	32
Poisson	806.4	440.2	145.3
Mean weight of beans (mg)	50.0	55.2	57.8

The high mortality in beans with more than one egg increases the selective advantage gained by females that avoid putting a second egg on a bean. To test for the pattern of oviposition, I isolated each of nine females on the day of her emergence and placed her with two males in a Petri dish (9 cm in diam) that contained more than 125 beans. The females lived for an average of 12.4 days (range 11–14) and deposited 59 to 102 eggs (mean 84.6 ± 4.17). There was no structural complexity in the Petri dish that could cause clumping. The beetles dispersed actively during the experiment and had free access to all the beans. If each egg was deposited independently, if all beans were equally available and equally attractive, and if the beetles moved around randomly, then the numbers of eggs on beans should follow a Poisson distribution.

The distribution of the eggs on beans departed from the Poisson in exactly the same way for all nine females, and all deviations were significant at the .001 level; hence, the summation of the individual distributions (Table 1) accurately portrays the patterns of oviposition by the individual females. There are fewer beans than expected with no eggs or with two or more eggs on them. These marked departures from the Poisson will occur only if the beetles search out and oviposit on beans with no eggs on them and reject beans that already carry eggs.

Eggs seemed to be placed on the heavier beans (Table 1), but more extensive data was needed for a test of the discrimination of beans by size. Larger containers were therefore set up with about 200 females and 10 g of beans for differing time periods, and three samples with means of 0.2, 1.1, and 1.8 eggs per bean were obtained. Each sample departed from the Poisson in the same way as the samples with single females. The eggs were uniformly arranged and, as exposure increased, the class around the mean that is excessively large shifted from 1 egg per bean to 2 or 3 eggs per bean (Fig. 2). These observations further show that the oviposition response cannot be the result of a fixed threshold reflex; the beetles must be rejecting or accepting beans

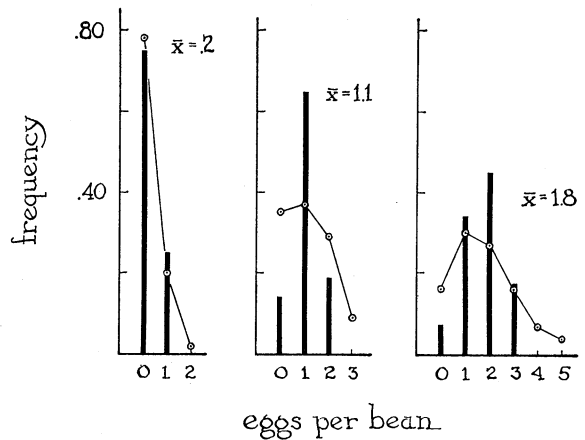


FIG. 2. Frequency distribution for beans carrying the specified number of eggs from three oviposition experiments. Differences in mean egg loads are due to length of exposure to a population of beetles.

as oviposition sites on the basis of the average number of eggs on beans at a given place and time.

The females not only discriminate beans on the basis of the number of eggs on a bean, but they also select beans according to weight (Table 1). This, too, is an averaging response, as illustrated by the fact that the mean bean weights always decline in each column and increase across the rows (Table 2). The mean weights for the samples with loads of 1.1 and 1.8 eggs per bean are all significantly different from other means in the same row or column but not significantly different from means on the diagonals of the table.

THE SURVIVORSHIP OF LARVAE

The benefits gained by *C. maculatus* at densities resulting in mean egg counts of less than 1 egg per bean are easily measured because bean weight is

TABLE 2. Mean weight and SE of the mean (in parentheses) of beans with the designated load of eggs. The beans are from the three samples plotted in Fig. 2. The differences between the means of each row and each column are statistically significant at least at the 5% level (Student-Neuman-Keuls test, Sokal and Rohlf 1969). The three groups of means along the diagonals are not significantly different

Mean no. of eggs per bean	Mean wt (mg) of beans with x eggs			
	0	1	2	3
0.2	49.6 (0.9)	56.8 (1.8)		
1.1	45.7 (2.6)	52.4 (1.2)	56.8 (1.9)	
1.8	33.4 (1.2)	44.9 (1.0)	50.0 (1.1)	55.6 (1.9)

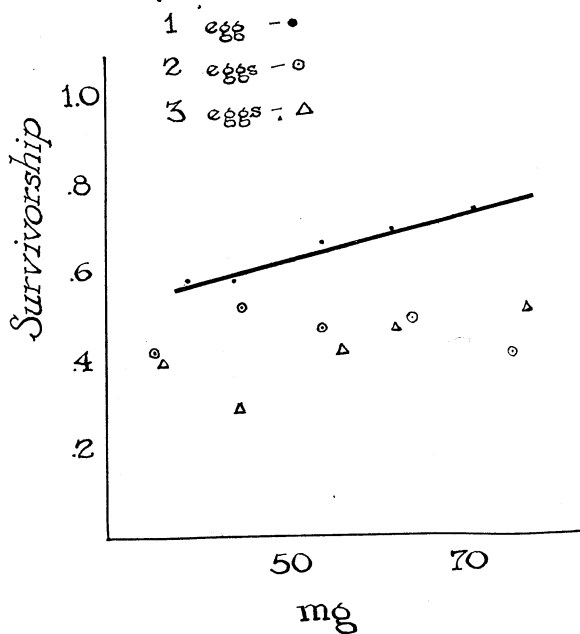


FIG. 3. Survivorship as a function of bean weight and number of eggs per bean. The correlation coefficient for the regression line for survivorship as a function of weight (survivorship = milligrams \times .005 + .368) is 0.976.

the only variable and survivorship is the frequency of emergences. A set of 131 beans each bearing one egg were separated into 10-mg classes and the results (Fig. 3) show a linear relation between bean weight and survivorship of the eggs. The regression accounts for more than 95% of the variation and establishes that there is a 0.5% change in fitness for each milligram difference in bean weight.

When two or three eggs are on a bean the survivorship shows no correlation with weight (Fig. 3). The results give an average fitness for all the eggs on a bean and there is no way to determine what went on inside the bean. This is troublesome because an evaluation of the selective pressures operating against females that add second or third eggs requires separate estimates of the survivorship of each egg. It is possible to obtain estimates for survivorship of the second (l_2) and third (l_3) eggs algebraically if the survivorship of the first egg is assumed to be the same as that of the single eggs (l_1 averaged over the distribution of beans given in Fig. 1 = 0.62). The mean survivorship for two eggs on a bean is

$$l_{1+2} = l_1 + l_2/2 = .464 \quad (\text{sample } n = 410)$$

$$l_2 = .308$$

and for three eggs it is

$$l_{1+2+3} = l_1 + l_2 + l_3/3 = .345 \quad (\text{sample } n = 107)$$

$$l_3 = .308.$$

This solution errs in assigning all of the mortality

from interactions to the second and third eggs and is, therefore, the minimum survivorship of those eggs.

As long as there are beans with no eggs on them, it is advantageous for females to avoid losing fitness by putting eggs on beans with no eggs on them. But the minimum survivorship of the second egg, .308, is great enough that it would be disadvantageous for the oviposition response to be determined by a simple threshold response that blocked oviposition on any bean with an egg already on it.

The averaging response, therefore, is an adaptation allowing a female to maximize fitness over a wide range of densities of eggs, and the different survivorship of second and third eggs are the basis for selective forces that can bring about the evolution of this response.

THE ANALYSIS OF THE OVIPOSITION STRATEGY

The estimates for survivorship show that departures from a pattern of random oviposition would increase the fitness of the female in two ways. At low densities (less than 1 egg per bean) there would be an advantage in selecting the largest beans first because survivorship increases by .005 for each added milligram of bean weight. Second, as the density of eggs per bean increases it is advantageous to avoid putting more than the mean number of eggs on a bean because survivorship sharply declines with increasing egg number. The empirical estimates of fitness can be used to define the tactics independently and to estimate the increased fitness of each tactic.

It is appropriate to use the yield from a Poisson distribution as an estimate of the performance of an unspecialized beetle. The perfect beetle (one with maximum fitness) would begin to exploit a universe of beans by putting the first egg on the largest bean and the second on the next largest, etc. To do this the female must first determine the dimensions of every bean in her universe and then make oviposition decisions. If the 184 beans in the sample with 0.2 eggs per bean (Table 2) are arranged in sequence of weights and the yield of adult beetles from the 46 largest beans ($\bar{x}_{wt} = 67.6 \pm 1.2$) predicted from the regression for l_1 it would yield 8% more than a random distribution would yield (Table 3).

The difference between the Poisson and the hypothetical tactic with maximum yields defines a scale that can be used to evaluate the strategy of the beetle; these comparisons are made in Table 3. Several combinations of adaptations are modeled and these show that a random pattern of oviposition would produce a higher yield than would the perfect beetle when the number of eggs per bean exceeds 1.0. This is because the survivorship of single eggs on beans is correlated with bean weight while the mean survivorship of two or more eggs per bean is

TABLE 3. A comparison of oviposition strategies. Yields of beetles from experiments (Fig. 2, Table 1) are compared to the yields from hypothetical distributions of eggs ranging from a random oviposition pattern (the Poisson distribution) to distributions that maximize yield by placing eggs on beans that are ordered from large to small. Weights of the beans from the experiments are used and the yields calculated from the survivorship estimates (Fig. 3). $\Delta\bar{w}$ is the change in fitness when compared to the Poisson

	0.2 eggs/bean		1.1 eggs/bean		1.8 eggs/bean	
	Yield ($\Delta\bar{w}$)	% of maximum	Yield ($\Delta\bar{w}$)	% of maximum	Yield ($\Delta\bar{w}$)	% of maximum
Poisson distribution	24.5 (0)	0	62.6	0	75.6	0
Observed frequency distribution with no weight discrimination	28.5 (1.16)	67	103.9 (1.66)	86	93.1 (1.23)	75
Observed distribution	29.7 (1.21)	69	103.8 (1.66)	86	92.7 (1.23)	75
Observed frequency distribution on beans ordered by weight	32.0 (1.31)	100	102.8 (1.64)	84	91.8 (1.21)	69
A uniform distribution on beans ordered by weight with the largest beans used first	32.0 (1.31)	100	108.7 (1.74)	96	93.8 (1.24)	78
A uniform distribution on beans ordered by weight with the second egg added to lighter beans	---	---	110.6 (1.77)	100	98.8 (1.31)	100

not correlated with weight. The perfect beetle should add the first egg to the largest beans first and when all the beans have one egg on them, the ordering of oviposition choices should be reversed and the second egg should be added to the smaller beans before the larger. This strategy is effective because the major component of survivorship for the second egg results from the first egg's dying so the second egg has the survivorship of a single egg. The mean deaths of the first egg are $1-l_1$ and survival of the second egg on such beans is $(1-l_1)l_1 = .296$. More of the value of l_2 is due to the failure of the first egg than to the weight of the bean. It is therefore best to use the smaller beans first when adding the second egg. This strategy would be effective at densities of 1 to 2 eggs per bean. Above 2 eggs per bean the optimization becomes a complex function of the differences in mean survival for various loads and could be solved by some clumping; hence, a uniform distribution will not optimize yields.

At densities below 2 eggs per bean the observed performance of the beetle generally yields over 70% of the maximum achievable. In terms of the gain in

fitness over the Poisson, this represents a 20%–60% gain in fitness (Table 3). As the estimated yield from a distribution with no weight discrimination shows, the greatest contributor to the yield is the nonrandomness of the distribution resulting from the ability of the female to count and estimate the average number of eggs on a bean. The discrimination of bean weight contributes to fitness only at quite low densities of eggs per bean.

THE ANALYSIS OF BEHAVIOR

The oviposition strategy outlined above is the result of a set of behavioral responses, but a direct analysis of oviposition behavior is difficult. A female deposits an average of 8 eggs per day; hence, oviposition is so infrequent that direct observations are impractical. It is clear that an oviposition decision must be preceded by an assessment of the densities of eggs and some measure of the size of beans. It would be most difficult to accumulate enough observations to discover how the beetle acquires the information needed to make oviposition decisions based on the average egg load and weight of beans.

TABLE 4. The basic commands for a program simulating the oviposition strategy of *C. maculatus*

Previous bean smaller	→ Present bean larger	}	Present bean with fewer eggs	→ OVIPOSIT
			Number of eggs equal	→ OVIPOSIT
			Present bean with more eggs	→ Reject
Previous bean larger or equal	→ Present bean smaller	}	Present bean with fewer eggs	→ OVIPOSIT
			Number of eggs equal	→ Reject
			Present bean with more eggs	→ Reject

TABLE 5. A comparison of the performance of *C. maculatus* with a computer simulation (Table 4). Pairs of means that are significantly different under a *t*-test are indicated by * = $P < 5\%$, or ** = $P < 1\%$. The frequency distribution for the sample mean of 1.1 eggs is significantly different from the simulation (chi-squared = 11.8, 2 df, $P < 1\%$)

Observed					Simulation				
Sample mean	Eggs/bean	Beans		Yield	Sample mean	Eggs/bean	Beans		Yield
		N	\bar{x} wt				N	\bar{x} wt	
0.2	0	138	49.6	29.7	0.2	0	815	50.6	22.3
	1	46	56.8*			1	189	54.8*	
						2	4	62.0	
1.1	0	26	45.7	89.5	1.1	0	212	48.4	79.4
	1	117	52.4*			1	519	50.1*	
	2	35	56.8			2	260	55.6	
	3	1	88.0			3	17	63.6	
1.8	0	5	33.4*	91.8	1.8	0	47	46.1*	90.4
	1	68	44.8*			1	307	47.9*	
	2	88	49.5			2	502	51.3	
	3	32	57.1			3	147	60.1	
					4	5	67.0		

It is much more practical to first use simulations to determine how much information the beetle may need to achieve the observed level of performance. The minimum information needed for averaging is a sample of two. If a sample of two is used it is easy to imagine the beetle as having a memory trace of the last bean she sat on and being able to compare that with the bean she is sitting on at present. The survivorship functions (Fig. 3) define the best decisions and these are detailed in Table 4. It is best to oviposit on a larger bean if it has the same number or fewer eggs on it, and it is best to oviposit on a smaller bean only if it has fewer eggs on it.

These simple commands were combined with a computer program that randomly drew and replaced beans from a bean population with a distribution of weights identical to the entire set of beans used in the set of experiments from which the data of Table 5 are taken. The results (Table 5) show a close correspondence of the observed distribution with the simulation. All three deviate from the simulation in a consistent fashion, and two of the three sets are not significantly different from the simulation. The observed distribution is always more uniform than the simulation. In terms of optimizing resource utilization (i.e., reducing the frequency of beans with below- or above-average loads) the beetle performs slightly better than the simulation. Some of the weight comparisons are significantly different and half these differences involve the sample with a mean of 1.8 eggs per bean (Table 5). The beans of that experiment had an average weight of 48.8 mg, significantly below the mean of 51.4 mg for the simulation sample. If the observed weights were

increased by 2.6 mg so as to have the bean samples comparable, then only the weights of beans with zero loads would be significantly different.

This adjustment would also make the modal class of all three observed samples consistently heavier and more frequent than found in the simulation. Such deviations will have an effect on the yield that can be estimated as was done for alternative oviposition strategies. The yield estimates show that the performance of the beetles makes the yield approximately 1% higher than that for the distribution from the simulation.

The statistically significant differences between the oviposition by the beetle and the simulated performance could be the direct result of beetles' being less precise in measuring the differences between beans. The simulation made decisions if there were differences of 1 mg. If the beetle discriminated less well that would increase the frequency with which beans were treated as being equal in weight and would therefore increase the frequency of rejections (Table 4).

The simulation is obviously the most parsimonious way to mimic the performance of the beetle, and it closely fits the performance of the beetles. It is reasonable to postulate that the beetle is likely to use the most parsimonious solution for maximizing its fitness.

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