What Is the Oviposition Decision Rule by Bean Weevil, *Callosobruchus maculatus*?

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Shwu-Bin Horng (1994) What is the oviposition decision rule by bean weevil, *Callosobruchus maculatus*? *Zoological Studies* **33**(4): 278-286. The oviposition decision of the female bean weevil is assumed to minimize the effects of larval competition and to maximize her lifetime fitness. A dynamic, stochastic model is proposed for bean weevil oviposition behavior analysis in terms of fitness maximization. The behavioral processes of the optimal females with varied levels of larval competition and females using other strategies (one absolute and two relative rules selected here) were simulated with the Monte Carlo simulation. The accepting probability of beans with varied egg loads, and the cumulative number of eggs laid by females using distinct strategies were compared. Lifetime fitness was used to analyse the effect of natural selection on the oviposition behavior of bean weevil. The real rule used by the bean weevil can be explored by comparing experimental data with this information.

Key words: Dynamic programming, Simulation.

The larvae of many bruchid beetles make no choices; they must feed, grow, and mature in a bean that was selected for them by their mother. If larval survival is affected by the size and quality of beans, selective pressures favor females that discriminate among beans and avoid overloading a bean (Mitchell 1975). For granivorous insects such as the bean weevil, *Callosobruchus maculatus*, a single ovipositing female maximizes her fitness by dispersing her eggs over the available seeds thereby minimizing the effects of larval competition between her offspring.

The oviposition behavior of this insect has been studied extensively; many reports have shown that the female can accurately assess the number of eggs on a seed and use this information to produce a near uniform distribution of egg loads (Utida 1943, Mitchell 1975, Messina and Renwick 1985, Credland et al. 1986, Wilson 1988). Although the cues controlling oviposition decisions include the number of eggs per bean that are discriminated accurately, there are still insufficient data to deduce how such information might be processed.

Mitchell (1975) proposed a simple digital model for release of oviposition behavior if a bean carries fewer eggs than the previous bean encountered. Wilson (1988) distinguished models based on fixed oviposition response (absolute models) from relative models in which cue interpretation based on past experience release oviposition behavior. He also proposed five sub-models. Absolute model A involves digital processing: an egg is added to beans with no eggs and the probability of laying an egg on a bean with eggs is 0.25. The probability of oviposition in Model B is the exponent of the negative number of eggs per bean. His relative models (C-E) call for oviposition decisions to be based on the relations between two of three measures, the measures being the number of beans visited, the number of beans encountered with no eggs on the bean, and the total number of eggs encountered.

There are two criteria according to which we can assess the correctness of these oviposition models. The model must generate egg dispersions resembling the observed dispersion, and the behavior of the beetle must correspond to expectations of the model (Mitchell 1990). Some of Wilson's models do not generate a uniform egg distribution, and as all strains are biased toward

hyperdispersion (some strains even disperse eggs uniformly, Messina 1990), these models cannot represent the real rules used by the beetles. Excluding the models that cannot generate a uniform distribution, one absolute and two relative rules are chosen for comparison in this paper. Strategy 1 is an absolute rule which takes into account the current egg load alone; the probability of oviposition is the exponent of the negative number of eggs per bean (Wilson 1988). Strategy 2 is a relative rule proposed by Mitchell (1975) which compares the number of eggs on the present seed with that on the previous bean encountered; the probability of oviposition is 1 or 0. Strategy 3 is also a relative rule, using the mean number of eggs per bean previously encountered for comparison; the probability of oviposition is the exponent of the negative number of eggs per bean divided by the mean number of eggs per bean plus one (Wilson 1988).

All three rules produce nearly uniform egg load distributions. Therefore, which is the real rule used by the weevil still cannot be determined. If we assume that the female oviposition decision is designed to minimize the effects of larval competition so as to maximize her lifetime fitness, then we can determine optimal oviposition decisions and expected lifetime fitness. The behavior of the optimal beetle is a standard criterion for comparison with other rules from an evolutionary view.

In this paper, we consider the bean weevils in a cultured or stored condition, as the hosts clump together in huge numbers, we also assume that the egg distribution is constant when the female beetle is ovipositing. The following questions are considered:

1. How does the optimal beetle behave? What is the optimal oviposition decision? What is the expected lifetime fitness of an optimal beetle?

2. What are the behavioral differences among females who use these three rules? What is the lifetime reproduction of a female who uses one of these three rules?

3. What is the influence of larval competition on the oviposition decision?

MATERIALS AND METHODS

For this investigation we used data from two bean weevil strains, South India and IITA, which have distinct larval competition and oviposition behavior. The survival of competing larvae in cowpeas with varied numbers of larvae competing in

a bean of these two strains is given in Table 1 (Mitchell 1990). We define fitness as the number of offspring accomplished by a female, the potential increments in fitness that the female acquires if she lays an egg on a seed with i eggs is assumed to be equal to the survival of competing larvae in a seed with one more eggs (i.e., $i + 1$ eggs).

We begin with a constant encounter probability reproduction model. The methods are adapted from Mangel (1987) and Mangel and Clark (1988). In a culture for experiments or storage, the female beetle invariably has many beans on which to lay eggs, and the female has only about ten eggs to lay each day (Wilson and Hill 1989). If we consider the behavior of one female in one day, then we can assume that the probabilities of the female encountering beans carrying distinct numbers of eggs are constant.

Description of state variables and their dynamics

We define a state variable X(t), which denotes the number of eggs remaining in a beetle's body at the start of period t. Because the female begins its adult life with a full complement of mature eggs, and since the oocytes mature the next day, the female has a full complement of mature eggs at the start of each day (Wilson and Hill 1989). The initial egg reserve is denoted X(0) = R. This is the number of eggs laid in one day.

We assume that the female encounters one of H + 1 kinds of beans which carry 0, 1, 2,...,H eggs/bean, and we define

$$\lambda(i) = \Pr\{\text{encountering a bean of type } i \text{ during one time period t}\}$$
$$i = 0, 1, ...H. \tag{1}$$

We also assume at most one encounter per period. Because the female lays an egg each encounter in a normal situation, the increment in fitness that the beetle accrues if it lays an egg on a host of type i is denoted W(i), assumed to be equal to survival of competing larvae in a host with $i + 1$ eggs. Nearly all beetles will survive the first five days (Bellows 1982), therefore we assume that the survival of the female between one period and the next is $\rho(t) = 1$. The time horizon T is set as the end of a day. Because the female has a constant oviduct capacity, and because she lays most eggs in the first five days (Wilson and Hill 1989), the conditions we set above accurately represent this beetle.

The expected lifetime fitness function F(x,t,T) is

$F(x,t,T)$ = the maximum expected lifetime
fitness obtained through egg
laying between times t and T,
given that $X(t) = x$.   (2)

At time t, the beetle has $X(t) = x$ eggs in her body; she encounters a bean carrying i eggs with probability $\lambda(i)$. If she accepts the bean for oviposition, one egg is laid; the fitness increases by $W(i)$ units, and the state variable becomes $X(t+1) = x-1$, otherwise it remains the same, $X(t+1) = x$.

Relating terminal fitness to state variables

The end condition is $F(x,t,T) = 0$, because there is no fitness associated with having any eggs remaining at the beginning of period T. If the eggs are not laid by the female before the end of the day, the initial number of eggs at the beginning of the next day remains the same (Wilson and Hill 1989).

The equation for lifetime fitness

The dynamic programming equation for $F(x,t,T)$ thus becomes

$$F(x,t,T) = \sum_{i=0}^{H} \lambda(i) \max \{\rho(t) F(x,t,T); W(i) +$$
$$\rho(t) F(x-1,t+1,T)\} \text{ for } x > 0$$
$$\text{and } F(x,t,T) = 0 \text{ for } x = 0. \quad (3)$$

The terms on the right-hand side of the equation are interpreted as follows. The summation is taken over all host types; $\lambda(i)$ is the probability that a bean of type i is encountered during period t. When a bean is encountered, the decision is to accept or to reject it. The first and second terms in brackets are the expected lifetime fitness of rejecting and accepting, and the second term is the sum of the immediate increment in fitness and the future expected lifetime fitness.

Pseudo-code for the solution

In order to solve the dynamic programming equation, we need the following computer program vectors.

(1). Two vectors of dimension R (the initial egg reserves) representing $F(x,t,T)$ and $F(x,t+1,T)$ which are defined as $F0(x)$ and $F1(x)$ respectively. (2). Vectors that characterize the host parameters. As we suppose that there are H + 1 possible types of beans, we need three vectors of dimension

H + 1. One is L that corresponds to the values of $\lambda(i)$; the second is W that corresponds to the values of $W(i)$ and the third is V that corresponds to the maximum expected lifetime fitness when a bean of type i is encountered. We also need a vector of dimension t, which corresponds to the values of $\rho(t)$. (3). A vector of dimension (R,H + 1,T) keeps track of the optimal oviposition decision.

The algorithm to solve the dynamic programming equation is adapted from Mangel and Clark (1988) and is as follows:

Step 1. Input the data of $\lambda(i)$, $W(i)$ for $i = 0$ to H and set $\rho(t) = 1$ for t = 1 to T.

Step 2. Initialize the vector F1(x), corresponding to the value of $F(x,T,T)$. We cycle through values of x, from 0 to R, and set F1(x) = 0.

Step 3. Cycle over t = T-1 to 1 and cycle over x = 0 to R again; then for each value of x also cycle over host types $i = 0$ to H; compute the expected fitness of rejecting and accepting the bean, fr and fa, and then compute $V(i) = \max(fr;fa)$. Set $D(x,i,t) = 1$ when fa > fr, otherwise $D(x,i,t) = 0$, and print the result. Continue cycling over all host types and replace F0(x) by $F0(x) + \lambda(i)*V(i)$. Then print F0(x).

Step 4. Again cycle over values of x. For each value of x, replace the current value of F1(x) by F0(x). This step updates the fitness function.

Step 5. Continue cycle over t to t = 1.

Pseudo-code for comparison of distinct strategies (Monte-Carlo Simulation)

The algorithm for the comparison of distinct strategies is as follows.

Step 1. Initialization step. The first step is to store the parameters $\lambda(i)$, $W(i)$ for $i = 0$ to H, the optimal decision matrix $D^*(x,i,t)$ (which is the optimal decision for a bean carrying i eggs encountered in period t when $X(t) = x$), and the initial egg complement of each insect. Here we assume that each of J females started with the same egg complement, and $X(J,1) = R$ for $j = 1$, 2, ..., J. Time is initialized by setting t = 1.

Step 2. Encounter step. Replace t by t + 1. Cycle over $j = 1$ to J, and draw a random number z. If $0 < = z < \lambda(0)$, then a bean of no egg is encountered in the current

period t. If $\lambda(0) < \, = z < \lambda(0) + \lambda(1)$, then a bean with one egg is encountered, and so on.

Step 3. Oviposition decision. Choose strategies for S = 1 to 4, and draw another random number z. Suppose that a bean of E eggs is encountered. When S = 1, the absolute rule is used, If $z < \, = \mathrm{EXP}(-E)$ then the female accepts the bean and lays an egg on it; otherwise, she rejects the bean. When S = 2, a relative rule is used. If the bean previously encountered has more eggs on it than the bean at present encountered, then the female accepts the bean; otherwise she rejects it. When S = 3, the other relative rule is used, if the bean encountered presents fewer eggs than the mean number of eggs previously encountered then the female accepts it with some definite probability; otherwise, she rejects it. When S = 4, the optimal oviposition decision is used. If a bean of type *i* is encountered by the "*j*th" insect during period t, then the oviposition decision is $D(X(j,t),i,t)$.

Step 4. Calculation of the accepting probability and the expected fitness. We define sume(*i*) and sumo(*i*) as total encountered and total eggs laid of host type *i*, thus the probability of accepting probability of type *i* bean is sumo(*i*) divided by sume(*i*). Suppose that the oviposition decision is O; replace the expected fitness, FITNESS, by FITNESS + $W(E)^*O$.

Step 5. Print the results. Print the accepting probability of beans with various loads of eggs and the expected fitness of period t. If t < T, update the insect's egg complement and return to step 2.

RESULTS

When the dynamic programming equation is solved, we obtain F(x,t,T), i.e., the maximum expected fitness through egg production between times t and T; more importantly, we also obtain the oviposition decisions as a function of time to go and current egg complement, for each type of bean that may be encountered. Here we use the data of two bean weevils strains, South India and IITA (Table 1). We assume that there are beans of four types each carrying 0 to 3 eggs per bean; the distribution of these beans is 0.25 for each.

Table 1. Potential fitness acquired by a female from laying an egg on a seed with *i* eggs (W_i) is assumed to be equal to survival of competing larvae in cowpeas with differing number of larvae competing in a bean (data from Mitchell 1990)

Eggs/bean (*i*)	W_i	
	IITA	South India
0	0.896	0.744
1	0.826	0.390
2	0.770	0.247
3	0.590	0.177
4	0.567	0.149
5	—	0.124

We also assume that the initial egg complement is 10 and the time to go is 20.

As the female invariably accepts 0-egg beans and rejects 3-egg beans except at the end of the time, Table 2 shows only the optimal oviposition decisions of South India and IITA strains on 1- and 2-egg beans under various conditions. The decisions alter with various state variables such as time to go, egg complement, and bean types. From the results, we predict the following. The insects accept beans carrying few eggs first, because they obtain higher fitness from them. For a fixed number of remaining eggs, older insects accept beans with larger egg loads that would have been rejected when younger. The beetle with fewer remaining eggs rejects the beans that the beetle with more remaining eggs accepts. Distinct strains should have distinct oviposition decisions, if they have varied larval competition.

The results of the dynamic programming equation give us characteristics for optimal insects. We compare these characteristics with those of selected models that we mentioned earlier. In order to test the hypothesis, Mitchell (1975 1990) and Wilson (1989) compared the final distribution of eggs generated from various models with experimental data. Although this comparison can be used to reject some hypotheses, many models that produce a uniform distribution (e.g., the models we chose) cannot be tested.

Given the oviposition decision rule or data, we use forward iteration to calculate the numbers of egg laid and the accepting probability of the beetle to the beans with various egg loads through time. These calculations give us more information than the final distribution of eggs.

Here we use the Monte-Carlo method to explore the behavioral processes of various models.

Table 2. Optimal oviposition decisions of two strains of bean weevil, South India and IITA

Obser-vation times	South India						IITA					
	$i = 1$			$i = 2$			$i = 1$			$i = 2$		
	$x = 10$	5	1	10	5	1	10	5	1	10	5	1
19	1	1	1	1	1	1	1	1	1	1	1	1
18	1	1	1	1	1	0	1	1	1	1	1	0
17	1	1	0	1	1	0	1	1	0	1	1	0
16	1	1	0	1	1	0	1	1	0	1	1	0
15	1	1	0	1	1	0	1	1	0	1	1	0
14	1	1	0	1	1	0	1	1	0	1	1	0
13	1	1	0	1	0	0	1	1	0	1	1	0
12	1	1	0	1	0	0	1	1	0	1	1	0
11	1	1	0	1	0	0	1	1	0	1	0	0
10	1	1	0	1	0	0	1	1	0	1	0	0
9	1	1	0	1	0	0	1	1	0	1	0	0
8	1	1	0	1	0	0	1	1	0	1	0	0
7	1	0	0	1	0	0	1	1	0	1	0	0
6	1	0	0	1	0	0	1	0	0	1	0	0
5	1	0	0	0	0	0	1	0	0	1	0	0
4	1	0	0	0	0	0	1	0	0	1	0	0
3	1	0	0	0	0	0	1	0	0	0	0	0
2	1	0	0	0	0	0	1	0	0	0	0	0
1	1	0	0	0	0	0	1	0	0	0	0	0

i is number of eggs per bean.
x is remaining eggs in the female's body.

Fig. 1. Accepting probabilities of beans with varied egg loads by the female of South India strain that uses an optimal oviposition decision.

Fig. 2. Accepting probabilities of beans with varied egg loads by the female of the IITA strain that uses an optimal oviposition decision.

We describe the computer experiments using the simulation approach. The conditions for the experiments are the same as those of dynamic programming, and 100 computer beetles are used for each simulation.

The probability of accepting beans with various egg loads through time is given in Figs. 1-5. The optimal insects accept beans of high potential (i.e., with fewer eggs) first, and accept beans of low potential only after some period of time. The accepting probability of beans with varied egg load alters with time, a greater probability to accept a bean of high potential declines with time. The reason is that some females have no eggs remaining in their body and reject the hosts. In contrast, the accepting probability of beans of low potential increases with time, and even the beans of least potential (e.g., 3-egg beans) are accepted with high probability at the end of time (Figs. 1, 2). The reason is that accepting beans of low potential is still better than rejecting them at the end of time. All these characteristics show that the optimal insects cannot use only the absolute rule for oviposition decision.

The South India strain and IITA strain have similar patterns of accepting probability to beans
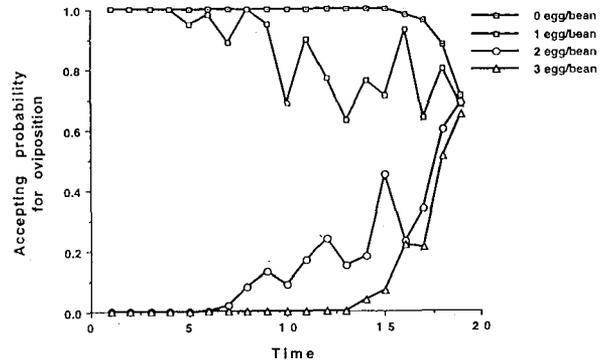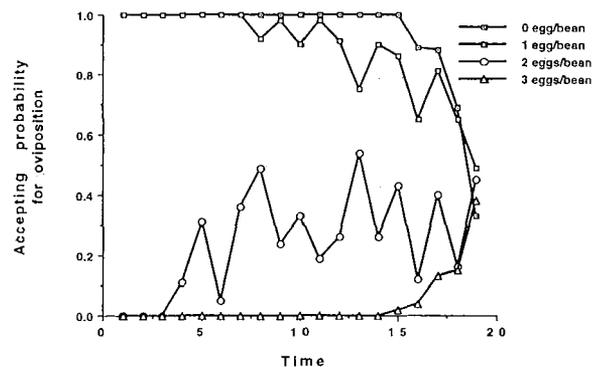
of the four types (Figs. 1, 2), but the IITA strain accepts 2-egg beans quickly and has a greater accepting probability than that of the South India strain through time. The reason is that the IITA strain has less larval competition than that of the South India strain. This behavior also explains why the South India strain disperses eggs uniformly, but IITA strain does not (Mitchell 1990).

The simulation results of strategies 1-3 for the two strains are nearly the same, and the accepting probability of various egg loads using strategies 1-3 are given in Figs. 3-5. Strategy 1 is an absolute rule, we find that the accepting probability of beans of four types are distinct from each other, but it maintains nearly a constant level through time for each type (Fig. 3). The reason is that the accepting probability of this model is influenced only by the egg loads of the encountered bean.

Strategy 2 is a relative rule, the beetle compares the most recently encountered bean with
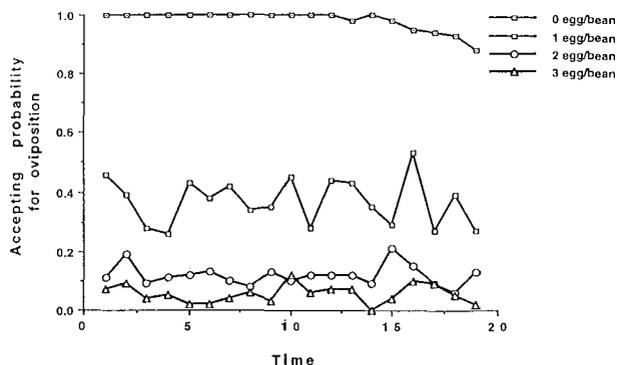
Fig. 3. Accepting probabilities of beans with varied egg loads by bean weevil females that use strategy 1 (an absolute rule).
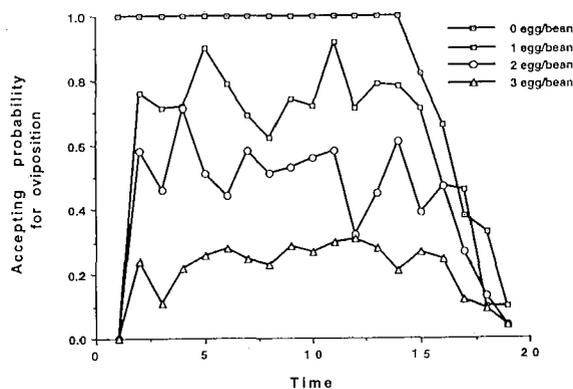

Fig. 4. Accepting probabilities of beans with varied egg loads by bean weevil females that use strategy 2 (a relative rule).

the present bean. According to our conditions, there are about 100, 75, 50, and 25 per cent beans that carry less or equal number of eggs on them for 3, 2, 1, and 0-egg beans. Therefore, we find that the accepting probability of beans of the four types fluctuate near these four levels (Fig. 4). Insects using this rule have a greater accepting probability of beans; therefore, after 15 encounters, many females have no remaining eggs and the accepting probability declines quickly.

Strategy 3 is also a relative rule, but the beetle compares the present bean with the mean egg number (m) of beans encountered previously. According to experimental conditions the mean egg number is 1.5. Therefore the beetle accepts all clean beans, and accepts 1- to 3-egg beans with a probability calculated according to the rule, $\exp(-i/m+1)$, at 0.67, 0.45, and 0.30, respectively.

The cumulative number of eggs laid by the optimal females of South India and IITA strains

and the females that use strategies 1, 2, or 3 are shown in Fig. 6. The optimal female of IITA lays more eggs than that of South India, which has severe larval competition. Only the female that uses strategy 2 lays more eggs than these two optimal females in the ovipositional process. The females of strategies 1 and 3 even fail to lay all their eggs before the end of the time.

The expected fitness of the females of the South India and IITA strains that use the optimal oviposition decision and strategies 1, 2, or 3 are shown in Figs. 7 and 8. The optimal insects invariably have the greatest expected fitness at the end of the time, but the insects using strategy 2 sometimes have the greatest gain of fitness in the process. The reason is that the insects using strategy 2 have a high accepting probability compared to the females that use other strategies.
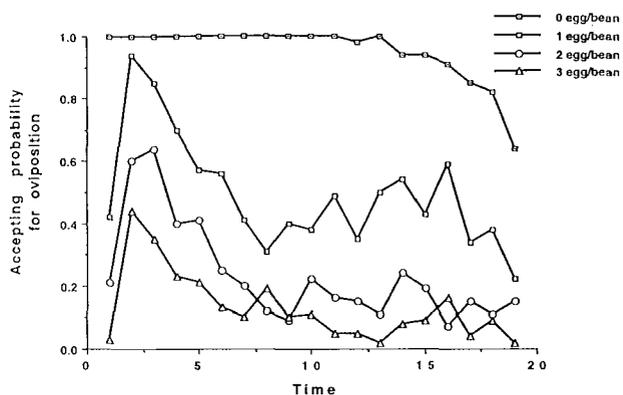

Fig. 5. Accepting probabilities of beans with varied egg loads by bean weevil females that use strategy 3 (a relative rule).
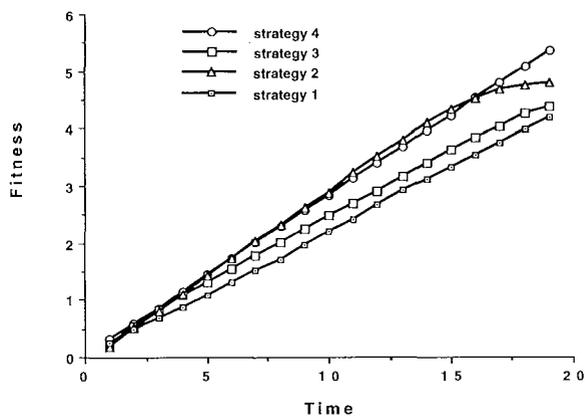

Fig. 6. Cumulative egg production by bean weevils of South India and IITA strains that use an optimal ovposition decision and three other strategies.
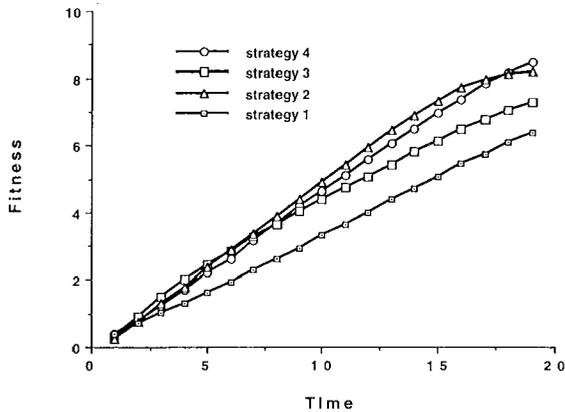
Fig. 7. Expected fitness of South India strain bean weevils that use the optimal oviposition decision (strategy 4) and three other strategies.
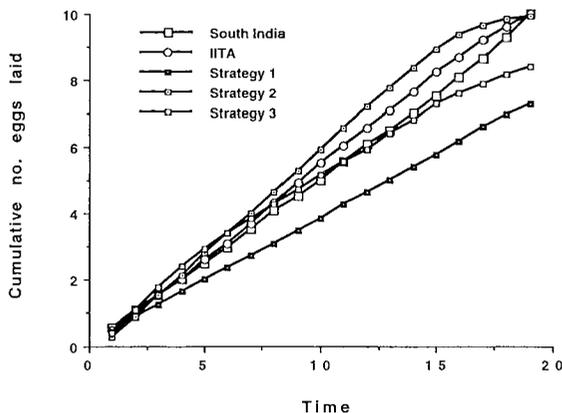

Fig. 8. Expected fitness of IITA strain bean weevils that use the optimal oviposition decision (strategy 4) and three other strategies.

Strategy 1 has a low accepting probability to a 1-egg bean causing the insect to have the lowest fitness in these two situations. Although the female of strategy 3 has a more effective memory trace than that of the female that uses strategy 2, she has no selective profitability. From these results, it seems that strategy 2 is suboptimal, but the behavior pattern of the female obviously remains distinct from that of optimal insects.

DISCUSSION

The main objective of this work was to explore how the information of egg distribution might be processed by bean weevils. We have discussed the behavioral processes of two strains of bean weevils

that use one of three strategies, or the optimal oviposition decision strategy. The optimal insect accepts high potential beans (0 or 1-egg beans) first, but accepts low potential beans later. The acceptance probability differs between optimal beetles of the two strains. No strategy generates the same behavioral pattern as the optimal oviposition decisions. The reason is that the oviposition decision according to these three strategies is determined only by the number of eggs per bean (e.g., the absolute rule) or egg distribution (e.g., a relative rule), and fails to consider the effects of larval competition on fitness. If oviposition decision behavior of the female is designed to minimize the effects of larval competition and maximize her fitness, then no strategy solves the problem. Therefore, if one strategy is to be used to describe the behavioral processes of the females that have varied larval competition and spacing behavior, the competitive coefficient factor must be incorporated into the model. For example, if the female can accurately assess the potential of beans with various egg loads, then the probability of oviposition on an n-egg bean for the female that uses the absolute rule should be the potential of a $(n + 1)$-egg bean to the potential of a 1-egg bean.

After simulating the behavioral processes of the beetle, we acquired the data of accepting probability of varying egg load with time. Using video equipment, we can measure these parameters and test the above mentioned models. Without this equipment, we can still set up the experiment and measure the number of eggs laid on beans of various types at some intervals, because in the processes of simulation we also generate these data, and they contain more information than just a measure of the final egg distribution (Mitchell 1975 1990). Because Lin (1993) showed that the probabilities of acceptance of a female bean weevil to beans with varied egg loads alter with time, the absolute rule cannot be the rule used by the female bean weevil.

The optimal insect considers not only larval competition and egg distribution on the host, but also the time needed to find acceptable hosts and the egg complement. In a definite time period, when the complement of eggs increases, the accepting probability increases to gain higher fitness. With the same egg complement and a longer period, the female has more chances to choose beans; hence the accepting probability of low potential beans decreases. There are data on egg complement (Bellows 1982, Wilson and Hill 1989), but none on the role of time.

For the convenience of simulation, we assume that there are equal numbers of 0, 1, 2, and 3-egg beans. Such a distribution of eggs will not occur in nature and the effect of egg distribution is not considered. When there are more high-potential beans, the optimal female rejects the low-potential beans more often. When low potential beans increase, the accepting probability of these beans also increases. When the average bean egg load is high, females that use absolute rules pass much time visiting beans that they subsequently reject. The females according to the relative rule use information about the egg distribution of their environment to make choices. Horng's model showed that the relative rule (strategy 2 here) is invariably best when searching time is limited (Horng 1993).

We did not consider the situation of dynamic egg distribution. When the number of beans is fewer, the egg distribution is influenced by oviposition of the females. Experimental design and observation are better suited for this condition (e.g., one female with ten beans) than that discussed in this paper; however, the formulation and solution of the dynamic programming equation becomes more complicated, though it may yield valuable information to explore the oviposition behavior of bean weevils. This should be studied in the future.

We still have insufficient data to explore which strategy is used by the female bean weevil. The analysis above has shown us the problems that can be solved by application of the various strategies, i.e., the female using a relative rule can obtain the information about the egg distribution, and the optimal insects also take the physiological conditions into consideration. The particular situation that the female bean weevils encounter may provide the information needed to explain why they should develop a specific strategy for oviposition decision. An integration of empirical and theoretical findings is needed to improve our understanding of this problem. This article may be regarded as a contribution to the theoretical basis.

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四紋豆象產卵決策法則之探討

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　　基於四紋豆象雌蟲的產卵行爲係在選汰過程中，爲減低幼蟲的競爭作用並使其適應值最佳化而發展的假設。首先建立一動態規畫模式以分析此種豆象的產卵行爲。接著進行蒙第卡羅模擬，以比較具不同幼蟲競爭程度時，最佳化雌蟲與採行絕對法則或相對法則雌蟲的產卵行爲過程。除比較採行上述各種產卵策略的雌蟲對具不同卵數寄主豆的接受機率及累積產卵數外，並以其適應值來比較自然選汰對不同產卵策略之作用。分析模式所得的資訊，經由試驗資料驗證，將可探明四紋豆象採行何種策略產卵，並明瞭此行爲發展之原因。

關鍵詞：動態規畫，模擬。

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