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Egg laying decisions by the bean weevil *Callosobruchus maculatus*

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ABSTRACT. 1. Previous work has shown that female *Callosobruchus maculatus* (F.) (Coleoptera: Bruchidae) can accurately assess the number of eggs on a seed and use this information to produce a near uniform distribution of egg-loads, so minimizing larval competition within hosts.

2. The decision to lay on a particular seed may be based on one of two possible rules: (i) a 'relative' rule, which compares the number of eggs on the present seed with that on previously encountered seeds; and (ii) an 'absolute' rule, which takes into account the current egg-load alone.

3. This paper describes an experimental study of oviposition behaviour which concludes that an absolute measure of egg-load probably determines egg-laying decisions. The implications of this result are discussed.

Key words. *Callosobruchus,* Bruchidae, oviposition behaviour, egg-load, bean weevil.

Introduction

Organisms which supply their progeny with a limiting resource after birth must make choices regarding division of the resource between offspring. For internally-feeding granivorous insects such as the bean weevil *Callosobruchus maculatus* (F.) (Coleoptera: Bruchidae), a single ovipositing female will maximize her fitness by dispersing her eggs over the available seeds so as to minimize the effects of larval competition between her offspring, provided that the fitness curve is convex at all clutch sizes below the Lack solution. In other words, she should disperse her eggs in an 'ideal free' way (Fretwell & Lucas, 1970). Such behaviour will result in a near-uniform distribution of eggs over the available seeds. This paper examines the mechanism by which this is achieved by testing two models for making egg-laying decisions.

Bruchids are pests of cultivated legumes and dried pulses. Although they infest crops in the field their impact here is minimal when compared with the severe and costly damage they cause to seeds in stores (Southgate, 1978, 1979; Jackai & Daoust, 1986). Females lay their eggs singly onto the surface of appropriate host seeds. After a few days the first instar larva hatches out of the egg and burrows into the seed, where it feeds and develops into a sexually mature adult. Individuals remain in the host seed chosen by their mother until emerging as adults. Adults do not feed and so must survive on reserves accumulated during larval development. Both individual survival and emergence weight are negatively correlated with the number of larvae per seed even at low larval densities (Smith & Lessells, 1985). Heavier females live longer and have higher fertility than lighter females. Thus,

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as the number of larvae already present in a seed increases, the gain in fitness to an ovipositing female from each additional egg laid, decreases (see Smith & Lessells, 1985, for review). The best strategy available to the female, then, is to lay first on seeds already bearing the fewest eggs, so producing a distribution of eggs on seeds which is more uniform than random. Several studies (e.g. Utida, 1943; Avidov *et al.*, 1965; pers. obs.) have shown that bruchid beetles do this.

The female requires a set of rules to decide whether or not to lay on each seed encountered. There are two basic types of rules that could be used: (i) a 'relative' rule, i.e. oviposition rate is determined by a comparison of the present egg-load with that of the previous seed(s) encountered, or, (ii) an 'absolute' rule, i.e. oviposition rate is determined solely by the current seed's egg-load.

There are many possible variations on these rules, each producing a different distribution of eggs on seeds. For example, the female may oviposit on a seed with a probability that varies continuously with current egg-load (fine discrimination), or she may distinguish only between pristine and egg-laden seeds, laying on the latter with the same probability regardless of egg-load (coarse discrimination).

Fig. 1 shows the distribution of egg-loads generated by computer simulations of a range of possible oviposition rules. In all of the simulations, seeds are visited at random and independently of their current egg-load. Only one egg is laid per oviposition visit. The computer simulations show that distributions which are more uniform than random can be generated by either absolute or relative oviposition rules. Moreover, rules in which the probability of laying an egg depends only on whether the seed is pristine or egg-laden, and not on the egg-load of egg-laden seeds, also produce more uniform than random distributions at low final egg densities. However, as expected, they do not function well at higher egg densities. The simulations show that a range of possible oviposition rules could be used by a female to achieve a uniform distribution of eggs over seeds; the aim of this study is to determine which rule is actually being used.

Previous models

Mitchell (1975) developed a model based on a 'rule of thumb' in which the beetle chooses between similar-sized egg-laden seeds by comparing the egg-load on the current seed with that on the last seed encountered. He suggested that the female should lay on the present seed only if it had fewer eggs than the last seed encountered. This is a somewhat crude relative rule, as the comparison the female makes is only between the last two seeds visited. Mitchell suggested that the beetles were also able to distinguish between seeds of different weights. However, because his experiments were performed at low egg densities he was not able to show whether females made a distinction between seeds with low or high egg-loads, only that they distinguished between egg-laden and pristine seeds. Mitchell produced a simulation of his rule of thumb and this compared favourably with data obtained from ovipositing beetles.

Messina & Renwick (1985a) showed that, in choice experiments, female *C.maculatus* were able to discriminate between very small differences in egg-load (0 eggs *v.* 1 egg; 1 egg *v.* 3 eggs; and 3 eggs *v.* 5 eggs) and preferentially laid on the lower egg-density seeds. They also demonstrated, by sequentially offering females batches of low (1 egg); intermediate (3 and 4 eggs); or high (5–12 eggs) egg-load seeds for 1 h at a time, that oviposition rate was strongly influenced by egg-load: females transferred from seeds with high egg-loads to seeds with lower egg-loads increased their rate of oviposition whilst the reverse transfer decreased it. Their experiments demonstrated that egg-load assessment is not coarse but that the beetles are 'counting' each seed's egg-load. They appear to do this using both chemical and tactile stimuli (Messina & Renwick, 1985b). The authors pointed out, however, that the rules governing the decision to oviposit were not clear from their results. Ovipositing females may be using a relative or an absolute rule. Although their results could not distinguish between the two strategies, Messina & Renwick were able to predict that if a memory trace of previously encountered seeds is used it must go back farther than just the previous seed, as females laid at a low rate for the full hour following transfer from low to high egg-load seeds.

Both Mitchell and Messina & Renwick appreciated that the actual egg-laying rule could only be found through a closer analysis of searching behaviour during oviposition bouts. In this way the number of seeds and the time

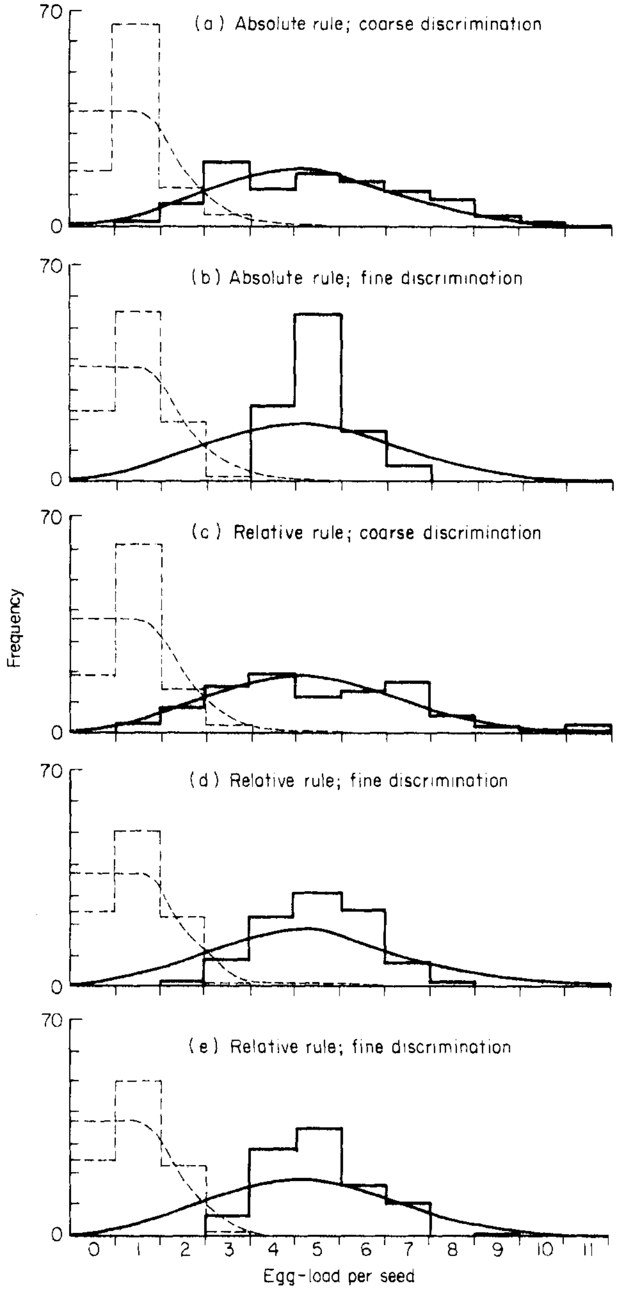

FIG. 1. Egg distributions generated by computer simulations of oviposition rules. Distributions were generated by Monte Carlo simulations of a single female ovipositing on 100 initially pristine seeds. Females visited (and re-visited) seeds at random, and at each visit laid an egg with a probability that was a function of the egg-load of the current seed, and, in the case of relative rules, of the egg-load of previously visited seeds (see below). Simulations were stopped after either 100 eggs (dashed lines) or 500 eggs (solid lines) had been laid. Histograms are examples of generated distributions; continuous curves are the expected (Poisson) distributions, when the decision to lay is independent of the current egg-load. All of the observed distributions, except for the 500-egg distributions in (a) and (c), differ from random (chi-square goodness-of-fit test). The following oviposition rules were used, where $p(\mathrm{lay})$=the probability of ovipositing on the current seed, c=the current seed's egg-load, m=the mean egg-load at encounter for all seed visits so far, and v=the proportion of seeds which were pristine at encounter for all seed visits so far. (a) If $c=0$, $p(\mathrm{lay})=1$. If $c>0$, $p(\mathrm{lay})=0.25$. (b) $p(\mathrm{lay})=\exp(-c)$. (c) If $c=0$, $p(\mathrm{lay})=\exp(-v)$. If $c>0$, $p(\mathrm{lay})=0.25\exp(-v)$. (d) $p(\mathrm{lay})=\exp(-c/(m+1))$. (e) If $c<m$, $p(\mathrm{lay})=1$. If $c>m$, $p(\mathrm{lay})=\exp(-c/(m+1))$.

involved in the process of egg-load assessment could be determined. This paper describes an experimental study in which observations of oviposition behaviour were used to test whether an absolute or relative rule was being used.

Testing the models

Ovipositing females were presented with a total of sixteen seeds, half of which bore just one egg and the other half a higher number of eggs: In 'low-density grids' the other half were all 5-egg seeds, and in 'high-density grids' all were 11-egg seeds. Thus the mean number of eggs per seed on the low- and high-density grids were 3 and 6, respectively.

It follows from the definitions for the two rules that if egg-load assessment is based upon a relative rule, then eggs should be laid on the 1-egg seeds at a higher rate in the high density grid than on the low. However, if only the present egg-load is involved in egg-laying decisions (an absolute rule), then the oviposition rate on the 1-egg seeds should be the same in the two grids (Table 1).

It also follows that in both grids oviposition should be at a higher rate on the 1-egg seeds than on the higher egg-density seeds, and that the oviposition rate on 5-egg seeds should be greater than that on 11-egg seeds. The overall oviposition rate results from a combination of the rate on the high-density seeds and on the low-density seeds. If an absolute rule is operating then the overall oviposition rate will be greater on low-density grids than on the high. However, no such predictions can be made if a relative rule is operating because the overall rate on the two grids is dependent on the exact form of the rule.

As a consequence of a decrease in the female's motivation to lay and/or of a shortage of mature eggs (pers. obs.), the rate at which *C.maculatus* oviposits, declines over time (e.g. Dick & Credland, 1984). This decline is evident even in the first hour of oviposition (pers. obs.), so where necessary it has been controlled for using analysis of covariance in comparisons between groups.

TABLE 1. Predictions for egg-laying rates in grids of high and low egg-density.

Seed type	Decision rule	
	Relative	Absolute
1-egg seeds	H>L	H=L
5/11-egg seeds	L>H	L>H
All seeds	?	L>H

H=oviposition rate in high-density grid (mean 6 eggs/seed); L=oviposition rate in low-density grid (mean 3 eggs/seed).

Materials and Methods

Culture methods

The stock cultures of *C.maculatus* were maintained on cowpeas, *Vignia unguiculata* (L.) Walp, in a constant temperature room at 30°C 35% r.h. with a 16L:8D photoperiod. The cultures were obtained from Imperial College at Silwood Park, Berkshire, and were derived from the populations used by Bellows (1982). These animals have been in culture for at least 100 generations and so can be considered as adapted to similar conditions which prevail in seed stores. Egg-loads reached a maximum mean of about 15 eggs per seed in culture.

In order to obtain seeds with suitable egg loads, newly emerged adults (0–12 h old) were collected from stock cultures 24 h prior to each series of tests. Varying numbers of these adults (about 16, 80 and 130) were placed in small plastic dishes (400 ml) containing approximately 100 cowpeas each, and allowed to oviposit for 24 h. The adults were then sieved out and the number of eggs on each seed counted until enough 1-egg, 5-egg and 11-egg seeds had been collected for that day's trials. Thus, all eggs used in experiments were less than 36 h old at the time they were used. As oviposition markers persist after egg shell removal (Messina & Renwick, 1985b) the required egg-loads were achieved naturally and not by scraping off surplus eggs.

Young, virgin females were required for each oviposition trial in order to ensure that no egg-laying had occurred prior to testing. Seeds containing adults ready to emerge were removed from the stock boxes approximately 5 h prior to the first test and placed in individual cells of a divided petri-dish. After 1 h, adults which had emerged during this time were removed and pairs (one of each sex) placed in 35 ml plastic pots without seeds and allowed to mate. Thus all females used in tests had not previously laid any eggs; were less than 1 h old prior to mating; and were mated to virgin males of similar age. In order to ensure enough time for mating to occur successfully and for maturation of the eggs within the newly emerged females, the pairs were left for at least a further 4 h. Preliminary experiments showed this method gave the most consistent results. Females were not anaesthetized prior to testing, and only the non-flying 'normal' phase adults were used in experiments. 'Active' form females, which emerge at high larval densities (Utida, 1972), were extremely rare in culture and were discarded, as were females which failed to lay within the first 20 min of a trial.

Experimental design

Sixteen egg-laden seeds were placed 20 mm apart on a clean filter paper divided into a 4×4 grid. Each row and each column of the grid contained two 1-egg seeds and two 5-egg or 11-egg seeds. Seed weight may be an important factor in a female's choice of oviposition site when seeds are without eggs (Mitchell, 1975; pers. obs.), therefore only egg-laden seeds were used. There was no difference in the mean weights of seeds with different egg-loads (as shown by random sampling). At the start of each trial the test female was placed, using a small paintbrush, into the centre of the grid, and an inverted 400 ml dish placed over the top to prevent escape.

The trial began when the female mounted the first seed and for the next hour the animal's behaviour was observed and recorded using a BBC microcomputer as a real-time event recorder. Each animal was used for just one trial, and trials on the low-density and high-density grids were performed alternately. A maximum of six trials per day was achieved. At the end of the trial, the number of eggs laid was confirmed by counting each seed's egg-load and comparing this with the figures recorded. There was no significant difference in the mean weights of females in each group.

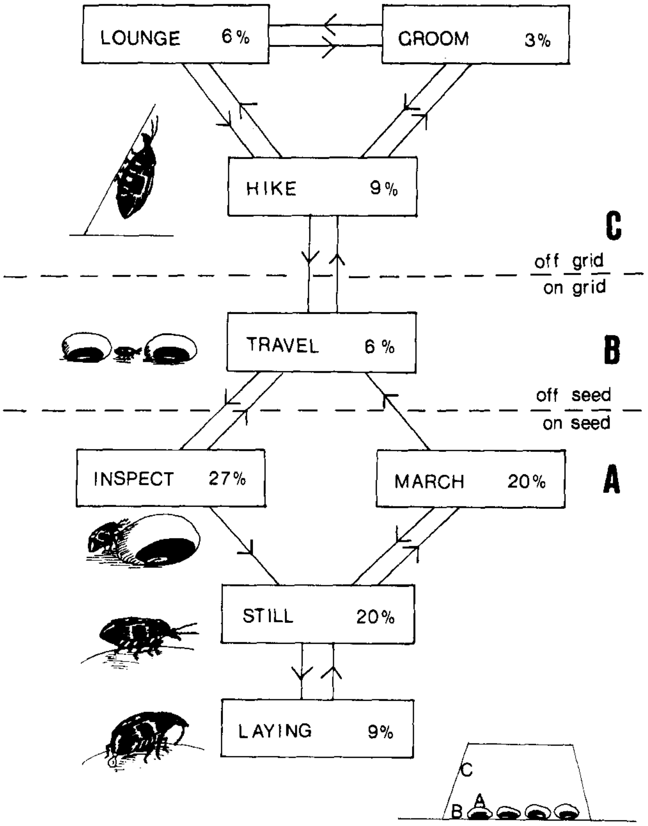

FIG. 2. An ethogram for ovipositing *C.maculatus*. Figures given are the mean percentage times spent performing each activity. There were no significant differences in these times between grid types.

Oviposition behaviour

Eight mutually exclusive behaviours (Fig. 2) were defined:

Inspect: time spent walking over a new seed before either stopping (usually prior to egg-laying) or leaving the seed.

Still: time spent motionless on the seed surface (usually before or after egg-laying).

Laying: time during which the female's ovipositor was more or less permanently extended.

March: time spent walking over the surface of a seed other than the initial inspect walk.

Travel: time spent on the arena floor between seeds.

Hike: walking outside the boundary of the grid, i.e. on the arena walls.

Lounge: time spent inactive on the sides of the arena.

Groom: time spent cleaning antennae and limbs (usually outside the grid boundary).

The oviposition behaviour sequence, for the purpose of calculating rates, was defined as the time spent laying plus any time spent motionless immediately prior to or following oviposition.

'Acceptance time' was defined as the time taken from arriving at a seed to starting oviposition behaviour.

'Rejection time' was the time spent on the seed surface in visits which did not result in an oviposition.

Using these definitions, egg-laying propensity was measured in the following four ways: (i) the probability of accepting a seed for oviposition: acceptance probability; (ii) the time taken to accept a seed for oviposition or to reject it: acceptance/rejection times; (iii) the number of eggs laid on each accepted seed; (iv) the number of eggs laid per seed encountered.

Each of these four variables was calculated separately for the 1-egg seeds and for the higher egg-load (5-egg/11-egg) seeds in both grids. Mean values were calculated using the average from each female for which a mean could be determined. Thus the maximum sample size for each grid mean (for figures given in Tables 2–6) was 16.

Results

Overall oviposition rate

Females on both the high- and low-density grids laid an average of 11 eggs during the 1 h trial (Fig. 3), the rate of egg-laying decreasing over the test period (Fig. 4). An analysis of covariance indicates that there was no significant

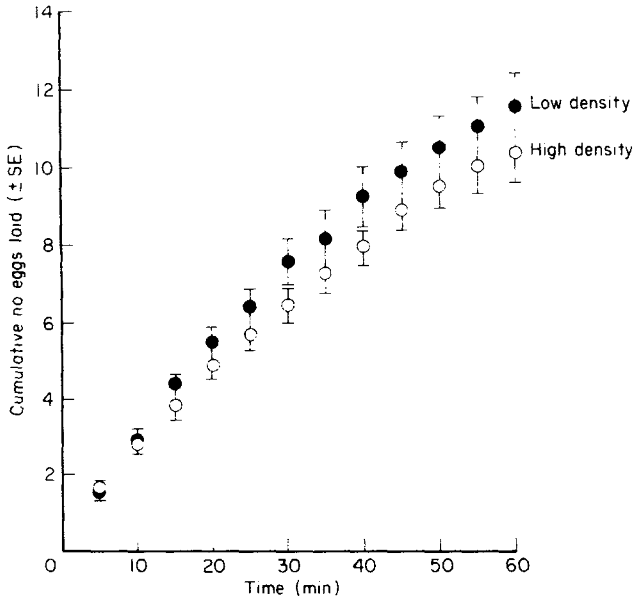

FIG. 3. Cumulative egg production by *C.maculatus* on high and low egg-density grids (means calculated using sixteen females for each grid type).

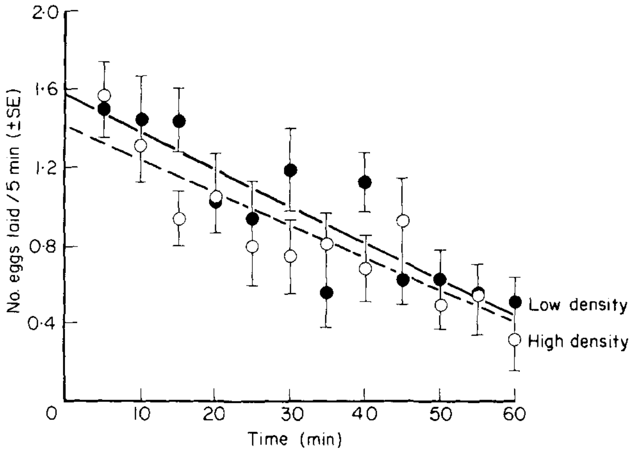

FIG. 4. Egg-laying rate by *C.maculatus* on high and low egg-density grids (means calculated using sixteen females for each grid type).

difference between the grids in the relationship between oviposition rate and time (ANCOVA: test for homogeneity of slopes: F(1,380)=0.2762, $P>0.1$; test of intercepts: F(1,381)=1.8308, $P>0.1$). If an absolute rule were being used, a higher overall rate of oviposition would be expected on the low-density grid than on the high. Although the difference is not significant, the regression line for the low-density grid is slightly higher than that for the high-density grid, therefore the absolute rule certainly cannot be discounted at this stage. No prediction can be made for a female using a relative rule (see Table 1).

Probability of seed acceptance

(a) 1-egg seeds. In both the high- and low-density grids the probability of accepting a 1-egg seed for oviposition shows an overall decline with time (Spearman rank correlation coefficients, $r_s \leq -0.246$, $N \geq 78$, $P<0.05$ for both grids, Fig. 5a), although an increase appears to take place during the last 10 min. After fitting a polynomial regression line to the arcsine transformed data, a dummy variable for grid-type explained little of the variance (T(153)=0.107, $P>0.9$). In other words there was no consistent difference between the acceptance probabilities for 1-egg seeds on the two grid-types. As the data are not normally distributed, this result was checked using a non-parametric test: none of a series of Fisher Exact Probability Tests, comparing the proportion of females from each grid-type which oviposited during each 10 min period of the trial, approached significance. The overall probability of acceptance for individual females did not differ between the grid densities (Table 2). It therefore seems safe to conclude that the probability of accepting a 1-egg seed for oviposition is independent of the mean egg density of the grid. This is consistent with the predictions based on an absolute rather than a relative rule (Table 1).

(b) *5-egg/11-egg seeds*. The probability of accepting 5-egg seeds for oviposition also declines with time ($r_s=-0.369$, $N=82$, $P<0.001$, Fig. 5b). However, no temporal change in acceptance times for 11-egg seeds was apparent ($r_s=-0.167$, $N=81$, NS). Both relationships are linear over the time period considered and differ in both slope and intercept (ANCOVA: test for homogeneity of slopes: F(1,159)=6.5747, $P<0.025$; test of intercepts: F(1,160)=6.4324, $P<0.025$). Checking this result using a non-parametric test, only for the first two 10 min periods of the trial were significant differences found in the proportion of females from each grid-type which oviposited (Fisher Exact Probability Test: $P<0.05$). A test of overall means also proved to be significant (Table 2). Thus there is a significant difference between the probability of accepting 5-egg seeds and 11-egg seeds, as predicted by both models.

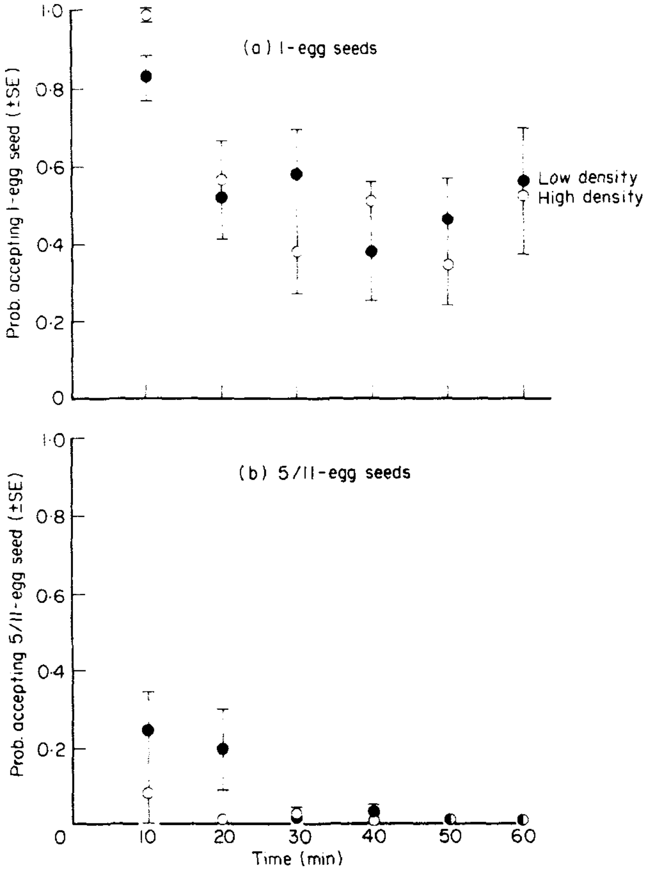

FIG. 5. Acceptance probabilities for seeds in high and low egg-density grids (means calculated using only females which inspected seeds during each 10 min period, therefore sample sizes vary between eight and sixteen for each grid type).

TABLE 2. Probability of accepting a seed for oviposition (mean ±SE [sample size]).

Seed egg-load	High-density grid		Low-density grid
1	0.46±0.07 [16]	(U=103; NS)	0.53±0.13 [16]
	(U=2; ***)		(U=0; ***)
11/5	0.02±0.01 [16]	(U=77.5; (*))	0.04±0.01 [16]

Mann-Whitney U test: NS, not significant; (*) $P<0.1$; * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

Seed acceptance/rejection times

(a) *Acceptance time.* The time between a female arriving at a seed and her laying an egg on that seed did not alter significantly during the course of each trial in either grid ($r_s \leq 0.192$, $N \geq 79$, NS). Analysis was therefore performed on the mean acceptance times for individuals during each trial.

There was no significant difference in the mean 1-egg acceptance times in the two grids. This provides further evidence that an absolute rule may be used by ovipositing females. As predicted by both rules, individuals took significantly longer to accept 11-egg seeds for oviposition than 5-egg seeds (Table 3). If females used a relative rule one would predict that they might take longer to accept 1-egg seeds on the low-density grid than on the high-density grid. Clearly, this didn't happen.

(b) *Rejection time.* There was no significant difference between the rejection times for the four seed types (Table 4).

Number of eggs laid per accepted seed

The mean number of eggs laid on accepted seeds did not alter significantly during the course of the trial in either grid ($r_s \leq -0.193$, $N \geq 79$, NS). The means for individual beetles in the two grids were therefore compared. Significantly more eggs were laid on accepted 1-egg seeds than on 5-egg seeds in the low-density grids (Table 5). There were no other significant differences. However, the small sample size for 11-egg seeds should be noted.

Mean number of eggs laid per encountered seed

The mean number of eggs laid per encountered seed is the product of the probability of seed acceptance and the number of eggs laid per accepted seed. There was no significant difference between the mean number of eggs laid on each 1-egg seed encountered on high- and low-density grids. However, significantly more eggs were laid on 5-egg seeds than on 11-egg seeds, and more on 1-egg seeds than on seeds with higher egg-load (Table 6). This is further evidence for females using an absolute rather than a relative rule.

TABLE 3. Time (s) to accept a seed for oviposition (mean ±SE [sample size]).

Seed egg-load	High-density grid	Low-density grid
1	67.7±8.1 [16] (U=120; NS)	60.0±3.9 [16]
	(U=4;*)	(U=69.5; NS)
11/5	125.3±23.4 [3] (U=2; *)	71.6±0.01 [16]

Mann-Whitney U test: NS, not significant; (*) P<0.1; * P<0.05; ** P<0.01; *** P<0.001.

TABLE 4. Time (s) to reject a seed for oviposition (mean ±SE [sample size]).

Seed egg-load	High-density grid	Low-density grid
1	18.1±4.9 [16] (U=84; NS)	22.0±4.4 [16]
	(U=77; NS)	(U=71 (*))
11/5	10.5±1.9 [16] (U=100; NS)	11.7±1.4 [16]

Mann-Whitney U test; NS, not significant; (*) P<0.1; * P<0.05; ** P<0.01; *** P<0.001.

TABLE 5. Number of eggs laid per accepted seed (mean ±SE [sample size]).

Seed egg-load	High-density grid	Low-density grid
1	1.71±0.16 [16] (U=105; NS)	1.51±0.16 [16]
	(U=13; NS)	(U=34; *)
11/5	1.33±0.34 [3] (U=12; NS)	1.30±0.24 [10]

Mann-Whitney U test; NS, not significant; (*) P<0.1; * P<0.05; ** P<0.01; *** P<0.001.

TABLE 6. Number of eggs laid per seed encountered (mean ±SE [sample size]).

Seed egg-load	High-density grid	Low-density grid
1	0.87±0.20 [16] (U=122; NS)	0.84±0.21 [16]
	(U=2;***)	(U=2;***)
11/5	0.02±0.01 [16] (U=79; (*))	0.06±0.02 [16]

Mann-Whitney U test; NS, not significant; (*) P<0.1; * P<0.05; ** P<0.01; *** P<0.001.

The trends presented above were determined on the assumption that a female's motivation to lay is dependent on time rather than the number of eggs already laid. Comparisons have therefore been made between groups, in various measures of oviposition rate, in relation to time. As a female's motivation to lay may instead be dependent on the number of eggs laid, the analyses were repeated comparing the various measures of oviposition rate in relation to the number of eggs laid. No differences were found between the two analyses; therefore only the time-dependent analysis is presented above.

Discussion

The results indicate that the overall oviposition rate declines over time, but at a similar rate for both grid densities. This is due primarily to a decline in the probability of accepting a seed for oviposition, rather than to a lengthening of the acceptance time or a decrease in the number of eggs laid on accepted seeds.

The probability of accepting a 1-egg seed for oviposition, and the time taken to accept the seed, do not differ between grid densities. However, females take longer to accept, and accept fewer, 11-egg seeds than 5-egg seeds. Once a seed has been accepted, the number of eggs a beetle will lay appears to be negatively correlated with the current egg-load of the seed.

The egg-laying rate on the 1-egg seeds does not differ between the two grid types. The oviposition rate on the 5-egg seeds is significantly greater than on the 11-egg seeds however. These results are consistent with the hypothesis that female *C.maculatus* are using an absolute rather than a relative rule in deciding whether or not to lay on a seed, that is, only the egg-load of the current seed, and not those of previously encountered seeds, influences the decision to oviposit. Not all relative rules are excluded though. For instance, the results do not exclude a rule in which the probability of laying on a seed with less than the mean egg-load is constant but decreases monotonically as the current seed's egg-load exceeds the mean for the environment (Fig. 1e). It would prove very difficult to perform the necessary experiments to make all of the distributions required in order to exclude the possibility of a relative rule being used by ovipositing females.

This study demonstrates the usefulness of behavioural observations to solve what are essentially behavioural problems. Previous studies on the oviposition strategies of phytophagous insects have concentrated on the end result of an oviposition bout to make inferences about the behavioural mechanisms operating (e.g. Mitchell, 1975; Messina & Renwick, 1985a). In the present study, oviposition rates were derived solely from the time spent making the appropriate egg-laying decisions, and hence are a more accurate reflection of *C.maculatus* egg-laying behaviour.

The results indicate that when assessing egg-load the beetles do not utilize information obtained during the course of the oviposition bout concerning mean egg-loads. A number of models have been developed in recent years to describe how animals, in a variety of situations, should use information about the mean utility of their environment to make choices about how to behave whilst within resource patches which form part of that environment (e.g. Charnov, 1976; Parker & Stuart, 1976; Cook & Hubbard, 1979; Smith & Lessells, 1985). Although very few studies to date have explicitly attempted to test these models, those which have (e.g. Krebs *et al.*, 1974; Hubbard & Cook, 1978; Waage, 1979), support the notion that decisions are dependent upon an assessment of the average utility of the environment (i.e. relative rules are used). However, Charnov *et al.* (1981) demonstrated that the sex ratio of offspring produced by the braconid wasp *Heterospilis prosopoidis*, which lays its eggs on the larvae of bean weevils, is dependent upon the age of the current host but is independent of the proportion of hosts of that age in the environment. Thus *Heterospilis* uses an absolute rule in deciding the sex ratio of its offspring.

Therefore, although absolute rules do appear to operate in nature, they are apparently very scarce. The reason for this becomes clear when one considers the simulations described earlier (see Fig. 1). At both high and low mean egg-loads finely-discriminating absolute rules produce very uniform distributions of eggs. However, when the average egg-load of seeds is high, females which use absolute rules spend much time visiting seeds which they subsequently reject. For example, in simulation (b) approximately 11,000 seeds were visited before all 500 eggs were laid, compared with about 1100 visits required in simulations (d) and (e). Hence, the egg-laying rate was slower when using an absolute rule rather than a relative rule.

There are several possible explanations for why *C.maculatus* uses an absolute rule. Firstly, if high mean egg-loads are uncommon in the natural environment, then the ability to respond to such a situation (and hence to evolve a relative rule), would not necessarily be selected for. However, bruchids have probably been associated with seed stores for several thousand years (Southgate, 1978), and so the natural conditions which this animal faces may be considered as similar to those which prevail in culture, where high egg-loads are the norm rather than the exception. Secondly, if the cost (in terms of time, energy, or egg-equivalents) of travelling between seeds is low compared to the benefits of producing a near-uniform distribution, then there would not be strong selection to reduce the number of unsuccessful seed visits. Thirdly, one may speculate that the neural apparatus required for an effective memory trace, a prerequisite for any relative rule, has a greater cost than any benefit of using a relative instead of an absolute rule. If this is true, then natural selection would favour individuals which used the 'cheaper' absolute rule.

Further studies are required before general statements can be made regarding the prevalence of absolute rules in nature and about the sorts of situations in which we might expect them to evolve.

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