Resource assessment and clutch size in the bean weevil, *Acanthoscelides obtectus*[†]

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Abstract: Bean weevil (*Acanthoscelides obtectus* (Say)) females were found to use seeds (discrete resource patches) differentially when different sizes were offered in multiple-choice tests. Females, either as a group or as individuals, laid significantly (two to six times) more eggs on large seeds than on those of five times smaller mass. In contrast, seed shape (flattened or spherical) did not contribute to clutch-size adjustment. Thus, *A obtectus* females seem to measure only relative seed size when a comparison is possible. Nevertheless, females overload seeds with eggs and this can result in larval competition, so that, whereas resource size assessment and a robust egg-load adjustment indicate a trade-off between resource use and female fitness, it does not seem to provide much benefit for the progeny in stored dry beans. Several features, eg the use of oviposition markers and its consequences, may counterbalance the possible negative effects. It is assumed that, due to life cycle differences, females in the bean field may realise different fitness gains in comparison with those living in stores.
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1 INTRODUCTION

Optimality theory predicts that, when the size of resource patches is limited, female seed beetles should assess the capacity of the resource when choosing a site for their egg-laying, and that clutch size should be proportional to the resource patch size. Thus, there is a trade-off between egg-load and female fitness.[1,2] This was shown to be the case with the bruchid beetle, *Callosobruchus maculatus* (Fabricius).[3] Females of the same species were shown to identify very small (one egg) differences in egg-load in choice experiments.[4] Two approaches to selection a site for oviposition have been suggested; comparison of the egg-load on a given seed with that on one examined previously and decision based on the number of eggs already present on a given seed, these being the relative or absolute rules (or comparison and threshold tactics),[5,6] respectively. Wilson[5] considered that *C maculatus* females used the absolute rule, whereas Horng[7] found that 75% of his sample used the relative and 25% the absolute rule. Females applying comparison tactics were observed to make fewer mistakes, possibly due to experience. Females of many insect species adjust clutch size to resource size,[1–3,8,9] although less is known as to which rule the female follows. However, some do not practice clutch size adjustment,[10] and adjusting egg-load according to resource size frequently involves host marking following oviposition.[11]

While many bruchid species glue eggs to the surface of seeds, bean weevil females (*Acanthoscelides obtectus* (Say), Coleoptera, Bruchidae) attach eggs to the surface only slightly, if at all; batches of eggs are laid randomly under seeds.[12,13] Because first-instar larvae have legs and move around to find a suitable site to enter a seed, it is important that the mother's decision as to site is governed by resource density, suitability of host and density of larvae. That adults of both sexes deposit oviposition-marking substances to cause a more uniform distribution of both eggs and first-instar larvae[14] is therefore intriguing. Yet overloading seeds with eggs, and as a consequence larval competition, is common in stored seeds. In contrast, some seed beetles, and *A obtectus* in particular, do respond to increased larval population level per unit resource with remarkable decrease in adult size.[15,16] The ability to modify rank-order preference through learning might be a further important factor in egg-laying decision[17] if a mixture of hosts is present (Szentesi Á, unpublished results). However, chance to select among a variety of available resources may not always beneficial since Bernays[17] showed that the reproductive performance of a generalist insect decreased in a mixture of host plants due to neural constraints.

Knowledge of the decision rules used in egg-laying by insect pests of stored products can enable better control strategies against them. Thus, the work

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reported here deals with resource use by the bean weevil, and, specifically, whether females assess seed size. Of interest were the following: whether females differentiate between seeds of different sizes (masses) in choice *versus* no-choice experiments; whether egg-load correlates with seed shape (spherical or flattened) and seed size; and whether individual females assess seed size differently when alone than when they are in a group.

2 EXPERIMENTAL METHODS

2.1 Test insects
The adult bean weevils (*A obtectus*) used in the experiments were from a laboratory rearing maintained on commercial beans at *ca* 26 °C and under a long day (18:6h light:dark) regime for at least 20 generations. They originated from a natural infestation developed on common beans *Phaseolus vulgaris* L.

2.2 Oviposition substrates
Two bean varieties were used, one was of unknown origin and the other was *P vulgaris* Kovácsházi gyöngy, the latter having 1000-seed weight of 164g. Both varieties had white and mostly spherical seeds. The unknown variety was used for a series of preliminary tests while the main, and all additional, tests were performed on the known variety. Individual seeds were weighed and allocated to one of five groups (seed mass classes; SMC) within the range of 50–250mg, each class containing seeds within a 10-mg band.

Each seed was uniformly positioned and its length, width and height measured (to within ±0.05mm) using mechanical callipers. The proportion between the smallest and largest measurement for a given seed was used as an indication of its shape (SMIMA),[18] the SMIMA value being aimed at giving a realistic measure as to how much the seed shape deviated from spherical. A seed with SMIMA < 0.600 was considered to have a flattened shape and one with SMIMA > 0.600 to be spherical. This classification was used to test the hypothesis that a combination of flatness and mass influences the number of eggs laid on a seed.

2.3 Test apparatus
Seeds were placed in a multiple-choice apparatus made from clear Plexiglass (Fig 1). It consisted of a base sheet (30 × 30cm) in which were 37 holes each holding a small glass container (12mm diameter × 10mm deep), above which were five identical Plexiglass sheets (3mm thick) with a 25cm diameter spherical opening in the middle; mounted on top of each other, they provided a space (*ca* 1.5cm high) above the glass containers. The apparatus was topped by a similar sheet but with a 3-cm hole in the centre, through which the test insects were introduced. The glass containers on the base were in a hexagonal formation with one container at each of the six corners and one in the middle. This pattern was repeated to give five replicate hexagonal seven-container sites, together with two empty sites so that there were seven (pseudo)replicates of five SMC in a single apparatus, together with two sites which always remained empty. Neighbouring containers were 17mm apart. The seeds were placed in the small glass containers and their position randomised according to a scheme for numbers 1 to 37. The cooled insects (see Section 2.4) were introduced into the test apparatus through the hole on the cover sheet. Under the hole was a small metal container fixed to hold the insects until they warmed up and slowly dispersed within the chamber. This precaution was taken to avoid biased egg distribution that could have happened if insects had been introduced directly onto the seeds and many had remained at the same place for a while. The glass containers and Plexiglass sheets were washed with a scentless detergent and rinsed with distilled water after each use. The glass containers were dried at 160 °C for a night before re-use.

2.4 Tests performed
In order to detect relative preferences, multiple-choice tests were applied. This type of test refers to an environment where selection among randomly arranged items of different qualities is possible through relative weighting of alternatives in a sequential decision process. Preference is used here as suggested,[19] ie it is the share of an object from a set of relative acceptances directed to all objects present.

As a general experimental arrangement, 1- to 3-day-old adults were removed from the laboratory rearing chamber, and seed debris removed by using an air stream. They were then cooled to 5 °C, and sorted into batches of 100 females and 10 males which represented one replicate. For each test, four sets of apparatus were used simultaneously. Insects were allowed to lay eggs for 3 days in a dark chamber at 25 °C. Following termination of a test the insects were removed and the number present (alive or dead) in the
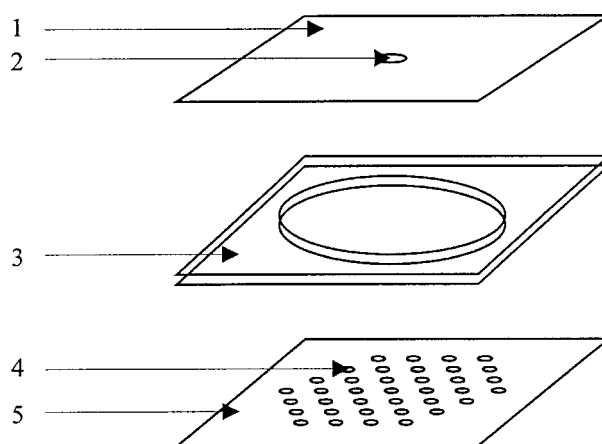

Figure 1. Schematic drawing of the multiple-choice test apparatus: 1=cover sheet, 2=hole for introducing the test insects, 3=sheets with identical-sized openings, 4=glass-containers holding seeds, 5=base-sheet with holes for the glass containers.

Table 1. Specifications of experiments

Expt	Replicates	Seed mass range (mg)	Mean (ranges) SMIMA	Number of insects used[a]	Remarks[b]
1	16	60–240[c]	0.624 (0.405–0.902)	100 f, 10 m	7 SMCs; preliminary; WRS
2	20	50–250[d]	0.621 (0.495–0.784)	100 f, 10 m	5 SMCs; main; WRS
3	4	60–70	0.503[e] (0.425–0.590), 0.665[f] (0.618–0.760)	100 f, 10 m	1 SMC; flattened and spherical
4	2	240–250	0.569[e] (0.495–0.594), 0.701[f] (0.672–0.738)	100 f, 10 m	1 SMC; flattened and spherical
5	5	50–60	0.595 (0.516–0.783)	100 f, 10 m	1 SMC; spherical only
6	5	250–260	0.650 (0.586–0.750)	100 f, 10 m	1 SMC; spherical only
7	25	60–260	0.628 (0.520–0.739)	1 f, 1 m	5 SMCs; WRS
8	21	150–160	0.652 (0.471–0.764)	1 f, 1 m	1 SMC; WRS

[a] f = female; m = male.
[b] SMC = seed mass class; WRS = without regard to shape. Seed mass increment per SMC.
[c] 30 mg.
[d] 50 mg.
[e] Flattened.
[f] Spherical.

glass containers was counted. The number of eggs laid under each seed was also counted.

2.4.1 Tests with SMC (Table 1; experiments 1 and 2)
To demonstrate whether female bean weevils were able to differentiate between SMCs, altogether 16 preliminary (7 SMCs) and 20 final (5 SMCs) tests were made.

2.4.2 Tests using a single SMC but seeds of different shape (Table 1; experiments 3 and 4)
Seeds within a single SMC but with either flattened or spherical shape were used (see mean SMIMA values, Table 1). One experiment involved four replicates of 60–70 mg seeds and another two replicates of 240–250 mg seeds (insufficient large seeds of one shape were available to allow greater replication).

2.4.3 Tests using one SMC and spherical seeds only (Table 1; experiments 5 and 6)
These experiments was aimed at ascertaining the effect, if any, of seed mass or shape in eliciting more egg-laying, and it served as a control for experiments 3 and 4. There were differences in SMCs in comparison with experiments 3 and 4, but they were not relevant since these experiments were performed with the knowledge that females do not discriminate between seeds in SMC groups differing by < 50 mg (Fig 2). Experimental arrangements were as with experiments 1 and 2 except that only one SMC (either 50–60 mg or 250–260 mg) was used throughout, with five replicates in each case.

2.4.4 Lifetime egg-laying response of individual females in tests using five and only one SMC (Table 1; experiments 7 and 8)
These experiments were designed to investigate whether oviposition responses showed the same trend with groups of bruchid *versus* individual females, ie whether, on the one hand, individual females actively selected larger seeds to lay more eggs or, on the other,

the group-level egg-laying responses (experiments 1–6) were due to disturbance by other females. Paper platforms were prepared on which five holes were harbouring the same glass containers used in the experiments described above. Seeds of 60–260 mg mass were used regardless of shape and they were randomised between the five sites. To show whether individual females visit and oviposit at each site even if SMC were unimportant, another series contained seeds of only one SMC (150–160 mg) at five sites. The numbers of replicates were 25 and 21, respectively. One 3-day-old male and one female were put into containers holding the seeds and the testing devices were covered with Petri-dish lids. Eggs were counted after 1 week, at which stage the majority of adults were dead.

2.5 Data analysis
Data from experiments 1 and 2 were not pooled, as the numbers of SMCs, the increment of mass change and the bean varieties were different. The trends, however, were compared. As experiments 1–6 had 7–35 replicates of one type of seed mass or shape per testing
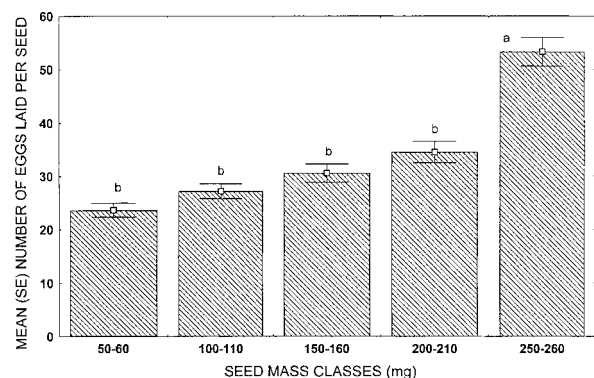

Figure 2. Egg-laying response of 100 *Acanthoscelides obtectus* females to five different seed mass classes (experiment 2). Different small letters denote significant differences at $P < 0.001$ (post hoc Scheffé-test following a one-way GLM ANOVA: $df = 1, 95$; $F = 19.31$; $P < 0.001$).

apparatus (pseudoreplicates), the numbers of eggs laid were averaged and only mean values were used for statistical calculations. The multiple-choice tests have a specific problem from the point of view of statistical analysis. The number of eggs laid on a given seed is not independent of eggs laid elsewhere as insects can move freely among seeds of different sizes. In other words, the condition of independence for treatments is not met, so that statistical tests based on this assumption are not recommended.[20,21] Due to the lack of appropriate tests, one-way GLM ANOVA and ANCOVA (with the latter SMIMA functioning as a covariate) were applied using seed mass as a categorical predictor to find significant effects. Means were compared by the post hoc Scheffé-test if ANOVA was significant. All data analyses were performed using the Statistica software version 5.5.[22]

3 RESULTS
Adult mortality during the tests was negligible.

3.1 Preference tests with SMCs
The preliminary test (experiment 1) with seven SMCs indicated (data not shown) that *A obtectus* females were able to differentiate among different seed mass classes when egg-laying. This experiment was repeated using five SMCs (experiment 2). A GLM ANCOVA test showed (Table 2) that seed mass significantly affected the number of eggs laid by 100 *A obtectus* females. Significantly fewer eggs were laid on seeds within the four lower mass (smaller) SMCs, than on the largest seeds (250–260 mg) (Fig 2). However, the seed shape (SMIMA) had no effect on the number of eggs laid (Table 2) even though the SMIMA values among the SMCs differed significantly (Fig 3: $df = 1,95$; $F = 116.000$; $P < 0.0001$). Although not influencing the number of eggs laid, seed shape was significantly correlated with seed mass (Pearson product-moment correlation; $N = 100$; $r = 0.73$; $t = 10.5$; $P < 0.0001$) and also with the number of eggs laid (Pearson product-moment correlation; $N = 100$; $r = 0.27$; $t = 2.83$; $P < 0.006$). However, it could be attributed to the character of the bean variety: in general, the larger were the beans, the more spherical they became.

3.2 Preference tests using only one SMC, but seeds of different shapes (spherical and flattened)
The shape of seeds, being either flattened or spherical,

in the range of 60–70 mg (experiment 3) or 240–250 mg (experiment 4) SMC, respectively, did not affect the number of eggs laid. The SMIMA values were significantly different in both cases: experiment 3: 0.503 (± 0.04) *versus* 0.665 (± 0.03) (flattened *versus* spherical) ($N = 4$; $df = 1,6$; $F = 116.3$; $P < 0.001$); experiment 4: 0.569 (± 0.02) *versus* 0.701 (± 0.02) ($N = 2$; $df = 1,2$; $F = 14572.7$; $P < 0.0001$). The number of eggs did not differ significantly by shape: experiment 3: 29.6 (± 2.3) *versus* 28.6 (± 2.4) ($N = 4$; $df = 1,6$; $F = 0.022$; $P = 0.886$); experiment 4: 39.6 (± 3.9) *versus* 22.9 (± 2.7) ($N = 2$; $df = 1,2$; $F = 9.77$; $P = 0.089$).

3.3 Tests using one SMC and spherical seeds only
Acanthoscelides obtectus females laid the same number of eggs on a single spherical SMC if tested alone, being either in the 50–60 mg or the 250–260 mg range (experiments 5 and 6). Although seed shapes (SMIMA) were selected to be as close to each other as possible, they still were significantly different: 0.595 (± 0.05) *versus* 0.650 (± 0.03) ($N = 10$; $df = 1,8$; $F = 466.3$; $P < 0.0001$). This could be a character of the bean variety used, as it tended to have more flattened seeds with decreasing seed mass (Fig 3). The number of eggs laid on the smaller SMC was the same as on the larger: 19.9 (± 0.9) *versus* 19.9 (± 2.1) ($N = 10$; $df = 1,8$; $F = 0.504$; $P = 0.4978$).

3.4 Egg-laying response of females in tests using either a single or multiple SMC sample
Comparison of Figs 2 and 4 indicates considerable similarity in distribution of eggs between seeds of different SMCs when only one (experiment 7) or a group of 100 females was present. However, the number of eggs laid differed significantly (Fig 4; one-way ANOVA; $N = 25$; $df = 4,120$; $F = 4.88$; $P = 0.001$) as did the frequency distribution of egg-laying females' responses (Fig 5). Females not only laid fewer eggs on seeds of 60–70-mg SMC than on other SMC groups

Table 2. One-way GLM ANCOVA table for experiment 2, if seed shape (SMIMA) is used as a covariant

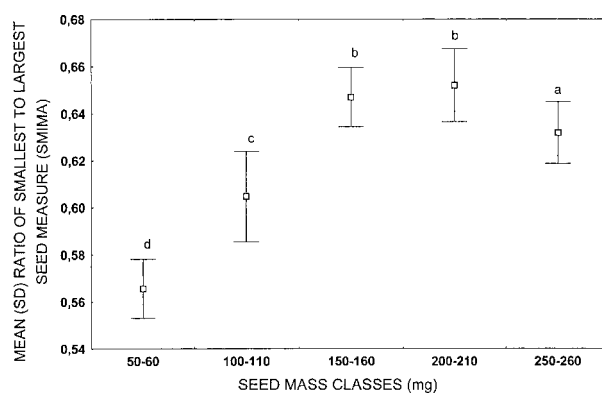| Effect	SS	df	MS	F	P
Intercept	273.69	1	273.69	1.9502	0.1658
SMIMA	75.72	1	75.72	0.5396	0.4644
Seed mass	9052.52	4	2263.13	16.1263	0.0000
Error	13191.74	94	140.338		

Figure 3. The 'shape' of the seeds used in the different seed mass classes (experiment 2). The shape (SMIMA) is given by the proportion of the smallest and largest measurement. The smaller SMIMA, the more flattened the seed. Different small letters denote significant differences at $P < 0.001$ (post hoc Scheffé-test following a one-way GLM ANOVA: $df = 1,95$; $F = 116.0$; $P < 0.001$).
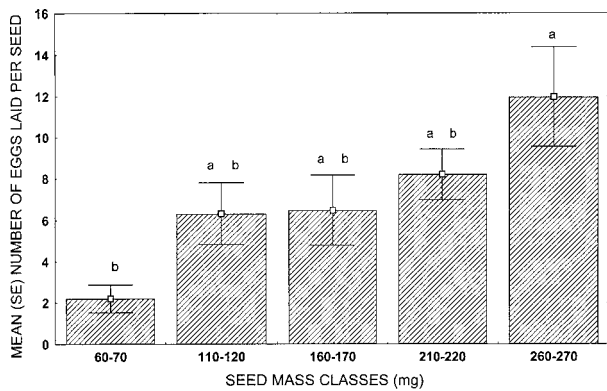
Figure 4. Egg-laying response of individual *Acanthoscelides obtectus* females to five different seed mass classes (experiment 7). Different small letters denote significant differences at $P < 0.001$ (post hoc Scheffé-test following a one-way GLM ANOVA: $df = 4,120$; $F = 4.88$; $P = 0.001$).

but also laid no eggs on 14 seeds. In contrast, they not only laid three times more eggs on the 260–270 mg-SMC seeds than on the small seeds, but also they ignored only three seeds in this case.

Within a replicate five-seed single SMC test (150–160 mg; experiment 8), the pattern of egg-laying did not differ significantly between replicates (one-way ANOVA; $N = 21$; $df = 4,100$; $F = 1.833$; $P = 0.128$) although females did not lay eggs on all the seeds within a replicate. Overall, the mean number of eggs was 8.1 (± 1.02) per seed per female.

4 DISCUSSION

The results indicate that *A obtectus* females, either as a group or as individuals, discriminate between small and large seeds in a choice situation, and adjust clutch-size accordingly: they lay significantly more eggs on large seeds and less on small ones (Figs 2 and 4). The distinction between SMCs, however, is not sharp, and certainly depends on the mass intervals chosen between neighbouring SMCs, as well as whether individual or group level responses are studied. Furthermore, females are not influenced by the shape of the seed in egg-laying, although larger seeds tended to be more spherical and smaller seeds were more
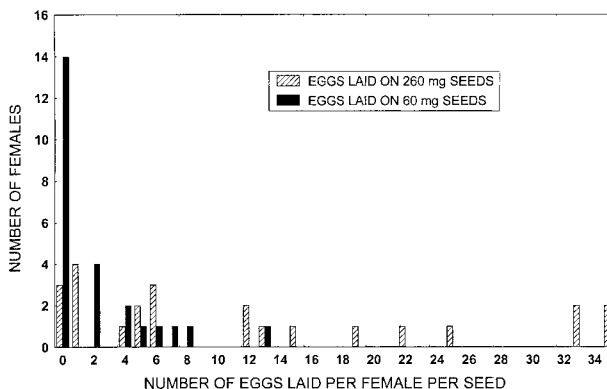
flattened (Fig 3). In two respective experiments (experiments 3 and 4) where seed mass was controlled and either flattened or spherical seeds were offered, females laid the same number of eggs on both shapes. Moreover, in respective tests having a single SMC and only one type of shape (experiments 5 and 6), females did not discriminate between small and large seeds either; they laid the same number of eggs.

Acanthoscelides obtectus seems to optimise egg-load by seed mass. The results obtained in this study are in accordance with others,[1–5,7–9] so far as resource size and egg-load adjustment are concerned. However, there are a number of specific features with *A obtectus* that make it difficult to assess the importance of such behavioural characteristics. Whether an *A obtectus* female behaves optimally when assessing resource size is highly dependent on the environmental context. It is a species with indoor and outdoor life cycles adapted to contrasting conditions. Under indoor conditions populations of bean weevils can reach very high density levels even on relatively small amounts of seeds. In such circumstances it is questionable whether individual seed-size assessment and clutch-size adjustment can be effective. As females do not attach eggs to seeds, and the first-instar larvae possess legs, they can disperse to find suitable seeds. Furthermore, adults mark the seeds which enhances egg and L1 dispersion.[14] In spite of all these, adults still lay a large number of eggs near seeds, which can result in severe larval competition. In this study, although females differentiated among resource sizes, they still laid 35 eggs on a single 260–270 mg seed, and 13 eggs on a 60–70 mg seed (experiment 7), many more than the seeds can support. It is, however, a feature of some bruchid species, *A obtectus* included, that even a high level of larval scramble competition does not necessarily end in death, as emerging adults can show substantial size reduction.[15,16,23] It was found that a threefold increase in larval population resulted in a 10% decrease in adult weight.[15]

From the above it seems that *A obtectus* females did not conform to behavioural rules when adjusting clutch size to resource size, because these were based on the number of eggs already present on respective seeds.[5,6] If the relative (comparison) rule were used a more even distribution of eggs would be found. However, if the absolute (threshold) rule were followed, overloading of seeds with eggs would be less frequent. None of these tactics was noticeable. It was shown that *A obtectus* females place eggs randomly among uniformly sized seeds,[13] and overload small seeds even when others nearby bear no eggs (Fig 5). Yet the results of this study indicate that females do conform to a behavioural pattern: they measure relative seed size (mass) if a choice is available and adjust clutch size accordingly. This, however, does not result in an egg-load proportional to seed size. Further specific features described above modify the outcome. It is possible that whereas some species, such as *C maculatus*, are highly adapted to storage circumstances

Figure 5. Distribution of individual females according to the number of eggs laid on 60–70 mg and on 260–270 mg seeds (experiment 7).

and have developed a series of behavioural traits to balance optimal resource use and female fitness, it may not be so with *A obtectus* in a similar situation.

In the field, in contrast with the above, *A obtectus* females seem to behave optimally at egg-laying, both assessing resource size and adjusting egg-load. The net recruitment of a new summer generation takes place in the field where females seek out the host. Encountering a bean plant, the female first thoroughly inspects the pod, circling around it. It is possible that she measures pod/seed size this way. Then she prepares an egg-laying hole on the pod and lays 10–15 eggs on the almost dry seeds or on the thin endocarp/septum separating the seeds.[24] As there is no possibility for a female to measure a seed's mass or size directly, because it is inside the pod, she must be making a decision on the basis of the pod's characters, eg its diameter, curvature and the like, that physically inform her on the resource size.[25] Unfortunately, the accurate selection process in the field has not yet been studied in detail. The resource-size selection can be optimal in the field because usually only a low level of infestation with no signs of larval competition is detected at harvest.

ACKNOWLEDGEMENTS

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