Oviposition decisions in the seed beetle, *Callosobruchus maculatus* (Coleoptera: Bruchidae): effects of seed size on superparasitism

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Abstract

The seed parasite *Callosobruchus maculatus* generally disperses eggs uniformly among seeds. We used cowpeas (*Vigna unguiculata*) of two class sizes (large and small) to test predictions based on a simple resource threshold model that females will distribute eggs among seeds in a manner that maximizes the amount of resources allocated to each offspring. When females were presented with multiple seeds of the same size, they tended to distribute their eggs relatively uniformly among seeds ($I \leqslant 0.27$ where I is the variance/mean ratio, and $I = 1$ reflects a random Poisson distribution). However, when seeds varied in size females distributed their eggs in a manner that maximized the amount of resources per offspring; females distributed eggs as predicted by seed differences in mass rather than as predicted by seed differences in surface area. Therefore, females must evaluate the relative quantity of resources available inside of a seed more accurately than if they compared the ratio of surface areas between seeds of varying size. Instead, females must either use cues other than surface area when estimating seed mass, or must have the ability to extrapolate non-linearly from surface area to seed mass. Females with higher egg loads (4-d-old females) laid more eggs when presented with seeds, but did not distribute their eggs less uniformly, than females with lower egg loads (1-d-old females), indicating that high egg load does not reduce female sensitivity to seed size and the presence of conspecific eggs. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The ability of parasitic insects to discriminate between hosts of differing quality can substantially affect their lifetime fitness. Hosts of many parasitic insects (such as parasitoids and seed beetles) are discrete and limited in size (van Alphen and Visser, 1990) and thus vary in their quality for parasite development and fitness (Mangel, 1989). When larvae cannot move among hosts, a female's oviposition decision determines the environment within which her progeny will complete development. Thus, oviposition decisions should be based in part on resource quality, with females preferring higher quality resources (Mitchell, 1975). When hosts are limiting, females must also choose between laying either clutches of eggs, laying additional eggs on previously parasitized hosts (superparasitism; van Alphen and Visser, 1990), or laying fewer eggs. Laying clutches and superparasitizing often come at the cost of reduced fitness per individual progeny, but have the benefit of increasing the number of progeny produced.

Optimality models predict that females should lay smaller clutches and be less willing to superparasitize on lower quality and/or smaller hosts (Godfray, 1987; Godfray et al., 1991; Mangel, 1992) because larval competition increases and progeny fitness decreases with decreasing host size (Fox et al., 1996). These predictions are generally consistent with findings in parasitic insects—females of most species prefer to oviposit on larger, higher quality hosts and generally lay smaller clutches on smaller and lower quality hosts (Schmidt and Smith, 1985; Takagi, 1986; Mitchell, 1990; Hardy et al., 1992; Vet et al. 1993; Fox and Mousseau, 1995). Here, we examine egg-laying decisions in the seed beetle, *Callosobruchus maculatus* (F.) (Coleoptera: Bruchidae) to test whether they conform to predictions of an optimality model.

C. maculatus is a parasite of dried seeds. Each seed is a discrete resource package, so that much of the biology of seed beetles is similar to the biology of parasitoids. Females can accurately access the number of eggs laid on a seed. When hosts are superabundant, females usually distribute their eggs uniformly (1 egg/seed) although the degree of uniformity varies among populations (Messina, 1989; Horng, 1994). However, when seeds are limiting most female *C. maculatus* readily superparasitize (i.e., lay eggs on previously parasitized seeds; Smith and Lessells, 1985; Wilson, 1988; Møller et al., 1989; Fox and Savalli, 1998; Mitchell 1975, 1990; Messina and Renwick, 1985; Credland and Wright, 1990; Mitchell and Thanthianga, 1990; Mbata, 1992a, b; Messina et al., 1992; Chiu and Messina, 1994; Horng, 1994, 1997; Wilson, 1994). In most populations, larvae compete via scramble competition without antagonistic confrontations (see Toquenaga and Fujii, 1990; Messina, 1991; Horng, 1997, for exceptions). Because seeds vary widely in size, these seed beetles provide an excellent system to test predictions concerning female oviposition decisions involving discrimination of resource quality and superparasitism. Seeds vary substantially in size, both within and among seed species, yet the effects of seed size on oviposition decisions has not been well examined. The two studies that have investigated effects of seed size suggest that females prefer smaller seeds (Avidov et al., 1965) or that the discrimination among seeds of variable size only contributes to fitness in low egg/seed densities (Mitchell, 1975). This is inconsistent with expectations of optimality models for superparasitic oviposition decisions.

In this study, we compare egg-laying decisions made by female *C. maculatus* to predictions of a simple resource threshold model (as adapted from Orians, 1969). This model predicts that there is some threshold in resource quality that favors repeated use of a discrete, higher quality resource over the use of a discrete, lesser quality resource. For example, imagine a female encounters two

seeds, one of size x, the other of size $2x$. Because the larger seed will provide her progeny with twice as much biomass as the smaller seed, she should lay her egg on the larger seed. However, if the $2x$ seed already bears an egg laid by another female, both seeds will provide the same amount of resource for the new larva because the resources in the $2x$ seed will be divided among the two larvae (assuming no antagonistic interactions within seeds, and assuming that the larva produced first does not have an advantage in garnering resources). If two eggs have already been laid on the $2x$ seed, and none on the x seed, then the x seed will provide more resources, and should thus be preferred. If there are two eggs on the $2x$ seed, and one egg on the x seed, females should prefer to oviposit again on the large seed. As egg density increases females should lay, on average, twice as many eggs on the $2x$ seed as on the x seed.

We report on three experiments in which we tested the hypotheses that (a) female *C. maculatus* distribute eggs relatively uniformly when they encounter multiple seeds of the same size; (b) they prefer to oviposit on larger seeds when encountering seeds of variable size; (c) female egg load affects female willingness to superparasitize; and (d) females distribute eggs among seeds in a manner consistent with predictions based on a simple resource threshold model in which seed mass is the indicator of seed quality. We also compare observed patterns of egg dispersion to the patterns predicted if females dispersed eggs according to relative surface area of seeds.

2. Materials and methods

2.1. Natural history

C. maculatus is a cosmopolitan pest of stored legumes (Fabaceae), particularly of the genus *Vigna*. Females cement eggs to the surface of the host (Messina, 1991). Larvae burrow into the seeds where their entire development (four instars plus pupal stadium) is completed. Larvae cannot move among seeds and are thus restricted to the seed that their mother has chosen for them. Beetles emerge from seeds reproductively mature. Emerging adults are well adapted to storage conditions, requiring neither food nor water to reproduce. Because beetles most commonly occur in seed stores, lab conditions do not significantly differ from their natural conditions.

2.2. Experimental population

The beetles used for our experiments were collected from infested cowpea (*Vigna unguiculata* (L.) Walpers) pods in Ouagadougou, Burkina Faso, in 1989 (details in Messina and Mitchell, 1989). This strain exhibits egg-laying behavior somewhat intermediate to most strains (Messina, 1993) leaning slightly towards the less strictly uniform egg layers, or "sloppier" (Messina and Mitchell, 1989; Messina et al., 1992) strains. There appear to be no antagonistic interactions within seeds; larval competition is primarily scramble (Frank Messina, pers. comm.).

2.3. General procedures

For one generation prior to the start of the experiment, beetles were reared at low density (1 egg/seed). These seeds were isolated to ensure that emerging beetles were virgin. All seeds were checked every 24 h for emerging adults. Thus, all females were $\leqslant 24$ h old at the initiation of each experiment.

Each emerging female was weighed on a microbalance to 0.1 mg precision and then confined with a single male. Copulation occurs almost immediately and males were removed immediately after mating. Females were then confined in a 35 mm Petri dish with seeds of cowpea (*V. unguiculata*) and allowed to lay eggs. The number and size of seeds presented, and the time that females were allowed to oviposit, varied among experiments and treatments as described below. All beetles were maintained prior to and during the experiments in a laboratory growth chamber at 25°C and constant light. All experiments were executed during a 2-month period in the summer of 1998.

So that we could differentiate individual seeds within dishes, seeds were dot-marked on the terminal ends with a Sharpie® ultra fine point pen. Preliminary data showed no effect of dots on female egg-laying decisions (see also Fox et al., 2001).

2.4. Experiment 1: Three large or three small seeds

In our first experiment, we tested the hypotheses that: (a) when encountering three seeds of similar size, females distribute their eggs relatively uniformly among them; and (b) females have higher realized fecundity when encountering three large seeds, indicating that they superparasitize more readily on large seeds than on small seeds.

To establish large and small seed treatments, cowpea seeds were weighed on a microbalance and separated into large and small size classes (large seeds, mean ± standard deviation 0.26 ± 0.02 g; small seeds 0.15 ± 0.02 g). Following mating, females were confined with either three large seeds or three small seeds ($n = 50$ per treatment) and allowed to lay eggs. Females were briefly disturbed at 2, 6, and 24 h to count the number of eggs laid on each seed; eggs were counted with a hand lens. After the 24-h count a single large seed or a single small seed was added to each dish. Females were allowed to lay eggs for another 2 h after which eggs were again counted on all seeds.

We tested for deviations from random egg distributions by calculating a variance/mean ratio for the number of eggs laid per seed ($I = s^2/X$; X = mean eggs per seed, s^2 = variance among seeds in the number of eggs per seed). I is an estimate of the degree of non-random egg laying, with $I = 1$ when eggs are distributed randomly, $I > 1$ when eggs tend to be clumped on one or two seeds, and $I < 1$ when eggs are tended toward a uniform distribution. I was calculated separately for each female, and then compared among treatments via a Mann–Whitney U-test. All statistical tests were performed using SAS (SAS Institute Inc., 1985).

2.5. Experiment 2: Simultaneous encounters with large and small seeds

This experiment was designed to test whether females distributed their eggs among seeds consistent with predictions of our simple resource threshold model. Large and small seeds were sorted as in Experiment 1 (large seeds, mean ± standard deviation, 0.26 ± 0.09 g; small seeds, 0.14 ± 0.02 g). Females were then confined with either: (1) one large and one small seed; (2) three large and three small seeds; (3) five large and five small seeds; (4) two large and one small seed; or (5) one large and two small seeds ($n = 50$ females in each treatment). Females in treatments 1, 2, and 3 were allowed to lay eggs for 48 h and eggs were counted at 2, 6, 24, and 48 h. Females in treatments 4 and 5 were allowed to lay eggs for 24 h and eggs were counted at 2, 6, and 24 h.

The predicted proportion of eggs that females should lay on large seeds, based on our simple resource threshold model, was calculated separately for each female as Σ (mass of large seeds)/Σ

(mass of large and small seeds). The actual proportion of eggs that females laid on large seeds was calculated as Σ (eggs laid on large seeds)/Σ (eggs laid on all seeds). Because some researchers have suggested that females may estimate seed mass using surface area, we estimated the proportion of eggs that females should lay on large seeds if they use surface area to measure size. Seed surface area was estimated empirically by measuring the area of the black eye portion of the seed. Because we are interested in relative size of large vs. small seeds, as long as the surface area of the black eye increases linearly with total seed surface area, it provides a suitable surrogate for measuring total surface area (which, due to seed shape, is very difficult to measure). Because the black eye region of the seed is largely flat and elliptical, its surface area is easy to calculate based on length and width (area $A = \pi l w$, where l and w are length and width). We estimated this surface area for 20 cowpea black eyes. Using a Model II regression (i.e., a geometric mean regression) in which we regressed log (surface area of the black eye) vs. log (seed mass) we found the exponent for the relationship between the mass of the seed and area of the black eye to be 0.67, exactly as expected based on the theoretical relationship between the surface area and volume of an elliptical object. We thus estimated surface area for all seeds assuming surface area increases at 0.67 times the rate of mass, and calculated the predicted proportion of eggs that females should lay on large seeds as Σ (surface area of large seeds)/Σ (surface area of large and small seeds).

Note that every seed was individually weighed such that predicted egg distributions were calculated separately for each female.

2.6. Experiment 3: Egg load effects on superparasitism rates

In this final experiment we tested the hypothesis that female egg load influences their willingness to superparasitize, such that females with higher egg loads will more readily superparasitize than females with lower egg loads. To manipulate egg load we manipulated female age. Because females continue to mature eggs in the absence of mating, we randomly assigned virgin females into two pairs of treatments ($n = 50$ females in each of the four treatments). In the first pair of treatments (1A and 1B), females were given a mate within 24 h of emergence from their host seed and, immediately following mating, were confined with seeds and allowed to lay eggs. In the second pair of treatments (2A and 2B), females were confined in a 35 mm Petri dish until they were approximately 4 d post-emergence. They were then given a mate and, following mating, were confined with seeds and allowed to lay eggs. In treatments 1A and 2A females were given three seeds of approximately equal size. Each seed had three eggs previously laid on it by another female. Thus, females in these two treatments were forced to superparasitize egg-laden seeds. As a control for the effects of female age on overall egg-laying rates, we confined females in treatments 1B and 2B with 10 clean seeds (no eggs on the seeds). All females were allowed to lay eggs for 2 h. The total number of eggs laid by each female during this 2 h period was recorded.

3. Results

3.1. Experiment 1: Three large or three small seeds

When females were presented with three large seeds they laid more eggs over all three time intervals than the females that were presented with three small seed (2 h, mean $\pm$ SEM, 2.62 ± 0.22

vs. 1.99 ± 0.20, Mann–Whitney U-test, $P = 0.02$; 6 h, 5.61 ± 0.30 vs. 3.42 ± 0.28, $P < 0.001$; 24 h, 7.77 ± 0.37 vs. 6.34 ± 0.35, $P < 0.001$; $n = 50$ females per treatment), indicating that females either less readily laid eggs on smaller seeds or were less likely to superparasitize smaller seeds. Regardless of whether they laid eggs on small or large seeds, however, females distributed their eggs fairly uniformly among the seeds (large seeds, $I = 0.27$, 0.20, and 0.17 for the 2, 6, and 24 h periods, respectively; small seeds, $I = 0.21$, 0.22, and 0.16). There was no evidence that the degree of uniformity differed among treatment (Mann–Whitney U-tests, $P > 0.50$ for each time period).

When a single seed (either large or small) was then added to each trial (after the 24-h count) and the female was allowed to oviposit for an additional 2 h, females added more eggs to the large seed than to the small seeds. When the original three seeds were large, females added on average 3.4 ± 0.3 eggs to the new large seed and 3.0 ± 0.3 eggs to the small seed ($P = 0.36$). When the original three seeds were small seed, females added an average 5.5 ± 0.5 eggs on the new large seed and 2.9 ± 0.3 eggs on the small seed (Mann–Whitney U-test, $P < 0.001$). On average, when females had been presented first with three small seeds they then laid more eggs on the new large seed than if they had originally been presented with three large seeds (5.5 vs. 3.4 eggs; $P < 0.001$). The size of the original three seeds did not affect the number of eggs laid on the new seed if the new seed was small (2.9 vs. 3.0; $P = 0.93$).

3.2. Experiment 2: Simultaneous encounters with large and small seeds

When females were presented with seeds of two sizes in equal proportions (one large vs. one small, three large vs. three small, or five large vs. five small) the proportion of eggs laid on the large seeds after 24 h averaged 0.62 ± 0.08, 0.63 ± 0.08, and 0.63 ± 0.08 for the one, three, and five seed treatments, respectively ($n = 50$ females per treatment). Likewise, when females were presented with the two sizes of seeds in unequal proportions (one large vs. two small or two large vs. one small) the proportion of eggs laid on the large seeds after 24 h averaged (corrected for the number of seeds) were 0.62 ± 0.07 and 0.61 ± 0.07, respectively.

The distribution of eggs among seeds at 2 h was not a very good fit to the expected distribution based on seed mass (Fig. 1). The distribution of eggs quickly converged on expectation over the next 22 h such that by 24 h females appeared to have behaved largely as expected based on our simple resource threshold model (Fig. 1)—in four treatments there was no significant difference between expected and observed egg distributions based on seed mass (Figs. 1A–D, t-tests, $P \geqslant 0.05$), although in one treatment (Fig. 1E; one large:two small seeds) females laid significantly fewer eggs than expected on the large seed ($P < 0.05$). The improved fit to the model across time coincided with a substantial reduction in the variance among females in the proportion of their eggs laid on the large seed (Fig. 2)—females appeared to converge over time on the same distribution of eggs. Although females tended to lay slightly fewer eggs on the large seed than expected based on our model (i.e., all deviations from predictions, by 24 h, are toward fewer than expected eggs), they laid significantly more eggs on the large seed than expected if they responded to surface area alone [t-tests: $P < 0.05$ for three of the treatments (Fig. 1A–C), $P \geqslant 0.05$ for only the one large:two small and two large:one small seed treatments (Figs. 1D and E)]. This demonstrates that females are better at judging seed mass than would be expected if they had extrapolated linearly from seed surface area to estimate mass.
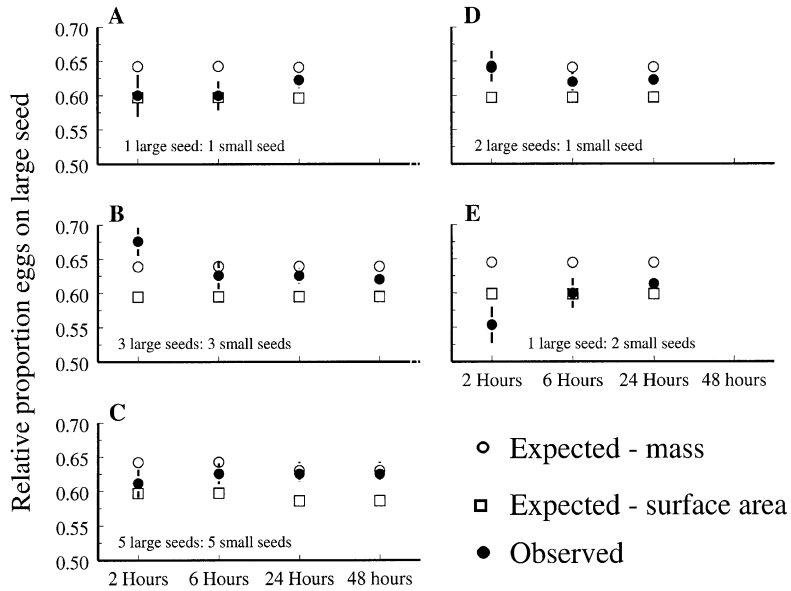
Fig. 1. The proportion of eggs laid on large seeds in the five experimental treatments. Egg proportions have been corrected for unequal numbers of large and small seeds in the two large seeds: one small seed and one large seed: two small seeds treatments. Note that females disperse their eggs among seeds according to the relative differences in seed mass rather than the relative differences in seed surface area.
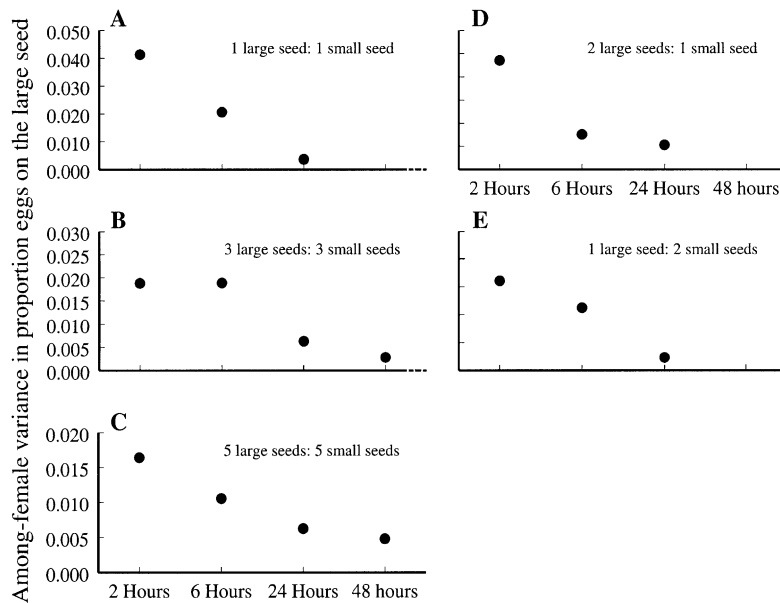

Fig. 2. Variance (among females) in the proportion of eggs laid on the large seed in five experimental settings.

3.3. Experiment 3: Egg load effects on superparasitism rates

Females that were 4 d old laid significantly more eggs on the previously parasitized seeds than did females that were $\geqslant 1$ d old (17.2 ± 1.0 vs. 8.5 ± 0.6 eggs laid in the 2 h test period; $P < 0.001$). Four-d-old females also laid substantially more eggs than 1-d-old females in the control treatments (presented with 10 seeds with no eggs on them; 25.3 ± 1.7 vs. 9.2 ± 1.3 eggs laid in the 2 h test period; $P < 0.001$), indicating that some of the increased number of eggs laid when exposed to egg-laden seeds may simply represent an increase in egg-laying rate. However, 1-d-old females only laid on average 8% fewer eggs when forced to superparasitize (compared to control females on 10 seeds), while 4-d-old females laid 32% fewer eggs. Because of the substantial difference in egg-laying rates and the resulting change in egg density within dishes throughout the 2 h test interval, this experiment is not adequate to distinguish whether 4-d-old females are equally or less willing to superparasitize relative to 1-d-old females. However, it does suggest that 4-d-old females are not less sensitive to egg densities (and thus are not more willing to superparasitize) than are 1-d-old females.

Four-d-old females also tended to distribute their eggs more evenly across seeds than did 1-d-old females ($I = 0.34$ vs. 0.56 for 4-d-old and 1-d-old females, respectively) although this pattern was marginally non-significant (Mann–Whitney U-test, $P = 0.06$). This is inconsistent with our expectation that 4-d-old females will be less sensitive to egg density when making oviposition decisions, but is consistent with our previous observation (e.g., Fig. 2) that the variance in egg distribution among seeds decreases as egg densities increase, tending toward uniformity when all seeds are of the same size.

4. Discussion

To our knowledge, this study is the first to examine seed size preference among seed beetles in relation to a resource threshold model. Our data suggest that female *C. maculatus* evaluate the relative quantity of resources available inside of a seed more accurately than if they compared the ratio of surface areas between seeds of varying size. They not only deposited more eggs on the larger seeds in Experiments 1 and 2, but distributed their eggs as predicted by our resource threshold model: according to the relative mass of the seeds available. The variance in the number of eggs laid per seed by females decreased over time. This may be due to lower fecundities early in the egg-laying period, and thus smaller sample sizes and higher variance among females. Alternatively, female discrimination among seeds may be less careful when egg densities are low, but as egg loads increase and superparasitism becomes unavoidable females discriminate more carefully.

Females distributed eggs in a manner inconsistent with the hypothesis that they base oviposition decisions on the relative surface area of seeds; they distribute eggs in a manner that reflects relative mass of seeds better than relative seed surface area (Mitchell, 1990). Instead, females must either use cues other than surface area when estimating seed mass, or must have the ability to extrapolate non-linearly from surface area to seed mass, allowing them to superparasitize seeds in an adaptive manner. Avidov et al. (1965) proposed that females identify seed size according to surface curvature. This hypothesis remains to be tested. Wilson (1988)

documented that female *C. maculatus* spend over a quarter (27%) of their ovipositional time inspecting the seeds but, other than oviposition pheromones and species–specific host plant cues, it is unclear what information females acquire during these bouts of inspection and how this information is processed by the female central nervous system.

Most research on optimal oviposition strategies of seed beetles has focused on the frequency of host encounters and the avoidance of superparasitism; the role of seed size is largely unconsidered. For instance, Mitchell and Thanthianga (1990) list three reasons that *C. maculatus* oviposition behavior deviates from randomness, none of which include variation in seed size. In our study, we found that not only is seed size important during oviposition but that it directs oviposition behavior away from a strict uniform dispersion. We have shown that variation in seed size is important during all oviposition periods and at varying egg loads, but suggest that it may be more important as oviposition time and egg loads increase. In another case, Mitchell (1983) recognizes female preferences for larger seeds when superparasitizing and cites Nwanze and Horber (1975a, b, 1976) as indicating the same, but the latter suggest that differences in seed surface area explain seed preference (contrary to our results and those of Avidov et al., 1965 and Mitchell, 1990).

In our study, we examined a single population of *C. maculatus*. However, populations vary in their host preference (Wasserman, 1986; Chiu and Messina, 1994), fecundity (Credland, 1986; Credland and Wright, 1989), egg-spacing behavior (Messina, 1989; Messina and Mitchell, 1989; Messina et al., 1992) and larval competition (Messina, 1991; Toquenaga, 1993; see Mitchell, 1990 for a review). The strain used in our study was intermediate to other strains in regards to egg-spacing behavior. Our experiment should be extended to other strains that have a stronger or weaker tendency to overdisperse their eggs, though we expect that seed size would have a similar effect because, as noted by Messina and Mitchell (1989), even the strictest overdispersing strains fail to maintain uniformity on larger hosts.

Our final experiment (Number 3) demonstrated that older females (relative to younger females) that were forced to delay oviposition more readily superparasitized egg-laden seeds. This suggests these older females are more motivated to lay on superparasitized seeds than younger females, presumably due to increasing egg load. That both sets of females deposited eggs evenly on equal-sized seeds suggests that the older females continue to assess and respond to resource quality even when extremely motivated to lay eggs; additional tests are needed to determine if older females react to seed size in the same manner as younger females.

The decisions of when and where to deposit eggs are very important to the lifetime fitness of parasitic insects. State-dependence (McNamara and Houston, 1996) and varied environmental situations produce inequalities that can influence female behavior. We have established not only a female preference for larger hosts in *C. maculatus*, but also that they superparasitize adaptively by assessing seed mass and distributing eggs among seeds according to their relative size.

considered alternative methods for estimating seed surface area. This research was funded in part by funds from the Louis Calder Center Summer Undergraduate Research Program (to J. Cope) and by NSF grant DEB-98-07315 (to C. Fox).

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