Influence of Seed Size on Exploitation by the Rice Weevil, *Sitophilus oryzae*

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Oviposition decisions and their fitness consequences for the seed parasite Sitophilus oryzae *(L.) (Coleoptera: Curculionidae) were investigated. Female* S. oryzae *lay eggs inside seeds such as wheat [* Triticum aestivum *(L.)]. Because larvae develop to adult within a single seed, the resources available are determined by the behavior of the female parent and characteristics of the seed in which the egg was deposited. Females were demonstrated to lay more eggs in kernels ≥20 mg. Females initiated the chewing of oviposition holes in shriveled kernels but were less likely to oviposit in them. Progeny size increased with increasing seed size, but the probability of an adult emerging was not affected. Females accepted large kernels more quickly than small kernels and this contributed to increased oviposition in large kernels. The increase in the number of eggs per kernel appears to result from an increase in number of visits resulting in oviposition rather than an increase in the number of eggs laid during a visit.*

INTRODUCTION

Seed parasites deposit eggs on or in a seed (i.e., host) and the progeny immature stage is completed within the same seed. Thus, the resources available to the larva are determined by the behavior of the female parent and the quality of the seed on which the egg was deposited (e.g., size, moisture, and presence of other larvae). Because seed size and competition among larvae

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can impact offspring survival and fecundity, to maximize fitness, females need to make decisions about which seeds to use, how many eggs to lay, and whether to lay eggs in hosts already parasitized. Much of the theoretical basis for these decisions was originally developed for parasitoid wasps (Godfray, 1994) and has been successfully applied to some seed beetles in the family Bruchidae (Mitchell, 1975; Messina and Renwick, 1985; Messina and Mitchell, 1989; Fox and Mousseau, 1995). The oviposition strategies of seed weevils in the genus *Sitophilus* have received less attention but generally do not fit optimality predictions and appear not to be adaptive (Smith and Lessells, 1985; Povey and Sibly, 1992).

Three species of *Sitophilus* [*S. granarius* (L.), *S. oryzae* (L.), and *S. zeamais* Mots; Coleoptera: Curculionidae] are seed parasites of cereal crops such as wheat, corn, rice, and sorghum and are important economic pest species in stored grain. The species share the same life history but do have a number of differences in their seed exploitation strategies (Longstaff, 1981). Females deposit eggs singly in holes excavated in the seed and typically leave the seed after laying a single egg (i.e., clutch of one) (Lathrop, 1914). Females do not oviposit into all excavated holes; some are abandoned and others are expanded into "feeding" holes. If an egg is laid, the weevil also deposits a mucilaginous egg plug to seal the hole. Females can lay multiple eggs per day and can lay a large number of eggs over their life span (Lathrop, 1914; Richards, 1947). The influence of factors such as seed species, variety, age, and moisture content, and environmental temperature and relative humidity have been shown to influence *Sitophilus* oviposition (Reddy, 1950; Davey, 1965; Russell, 1968; Singh *et al.*, 1974; Pederson, 1979; Kanaujia and Levinson, 1981; Urrelo and Wright, 1989).

Higher-quality seeds, determined in part by seed size, are expected to offer greater fitness benefits such as greater probability of larval survival, larger progeny size, and support for larger numbers of progeny than smaller seeds. Parasitoid wasps have been demonstrated to measure host size and adjust the number or sex of eggs that they lay in response to host quality (e.g., Schmidt and Smith, 1985; Takagi, 1986; Godfray *et al.*, 1991). Some species of bruchid weevils have been demonstrated to prefer large seeds for oviposition and to lay larger clutches in larger seeds (e.g., Mitchell, 1975; Fox and Mousseau, 1995). *Sitophilus* spp. have also been reported to prefer large seeds for oviposition; larger seeds were more likely to be parasitized or contain more than one egg than smaller seeds (e.g., Ewer, 1945; Segrove, 1951; Tyagi and Girish, 1975; Pederson, 1979; Stejskal and Kučerová, 1996).

Female *Sitophilus* spp. will lay eggs in seeds already parasitized by conspecifics (i.e., superparasitism), even though typically only a single individual or possibly two will emerge from a seed (Richards, 1947; Pederson, 1979; Giga and Smith, 1985). Superparasitism does not necessarily mean that the

female cannot discriminate parasitized from unparasitized hosts, because under some conditions superparasitism is favored by natural selection (Salt, 1961; van Lentern, 1981; van Alphen and Nell, 1982; Waage and Godfray, 1985). Some bruchid seed beetles produce oviposition markers and avoid ovipositing in seeds containing conspecifics (Avidov *et al.*, 1965; Messina and Renwick, 1985; Credland and Wright, 1990; M'Bata, 1992; M'Bata and Ramaswamy, 1995), but *Sitophilus* spp. do not appear to produce or respond to oviposition markers (Segrove, 1951; Giga and Smith, 1985; Fava and Springhetti, 1991). Everything else being equal, females should oviposit in seeds that have the fewest eggs, resulting in a uniform distribution (Mitchell, 1975; Smith and Lessells 1985). Some bruchid beetle species tend to have a more uniform distribution of eggs among seeds (Avidov *et al.*, 1965; Mitchell, 1975), but *Sitophilus* spp. tend to have an aggregated distribution (Richards, 1947; Segrove, 1951; Smith and Lessells, 1985; Nardon *et al.*, 1988). More than one egg per seed can lead to larval competition and mortality (Smith and Lessells, 1985).

Sitophilus spp. oviposition behavior has been reported to be maladaptive, but the mechanisms and fitness consequences of different oviposition decisions are not well understood. In part this is because research on *Sitophilus* oviposition behavior has tended to emphasize population level effects such as egg distribution, with few studies addressing individual female oviposition behavior and its fitness consequences. In addition, much of the early research on *Sitophilus* behavior is difficult to interpret due to lack of detail, experimental design and analysis flaws, and uncertainty of species designations (Longstaff, 1981). The objective of these experiments was to determine how *S. oryzae* oviposition decisions and their fitness are influenced by seed quality [i.e., hard red winter wheat, *Triticum aestivum* (L.), kernel size].

MATERIALS AND METHODS

Newly emerged *S. oryzae* from a laboratory colony were sexed based on rostrum characters (Halstead, 1963) and paired with males for at least 1 week prior to initiating experiments. Females were exposed to single wheat kernels in the dark at 25°C for a 17-h period. Between exposures to individual kernels, typically 7 h, females were held in 30-ml plastic cups with approximately 4 g of mixed-size wheat. Individual females were exposed to five kernel size categories in randomized order and the exposures were repeated three times for each female. There were 40 females tested (two blocks of 20 females each). Average value for each individual weevil and kernel category was used for data analysis.

Five categories of hard red winter wheat kernels (unknown variety) based on weight or condition were used in experiments. All categories were sorted individually from the same wheat sample to control for varietal variation. The categories of wheat kernels were as follows: category 1, shriveled kernels; category 2, plump or unshriveled kernels, <20 mg; category 3, between 20 and 30 mg; category 4, between 30 and 40 mg; and category 5, >40 mg. The wheat kernels in each category were also characterized in terms of length and width (100 kernels in each category), percentage moisture based on oven drying, protein content standardized to 14% moisture using NIR analysis (>150 kernels), and hardness based on single-kernel characterization (SKCS 4100) analysis (>150 kernels).

After exposure to females, wheat kernels were transferred to multiwell plates and held for 2–4 days. The kernels were then individually stained using acid fuchsin (Frankenfeld, 1948; Pederson, 1979). After drying they were inspected for weevil damage. The types of seed exploitation by females were divided into three categories: oviposition holes [chewed cylindrical hole that is slightly larger than the diameter of weevil snout, i.e., egg-laying cavity (Kanaujia and Levinson, 1981)], egg plugs [oviposition hole in which an egg and egg plug have been deposited, i.e., egg cavities (Kanaujia and Levinson, 1981)], and feeding holes [chewed holes that are irregular in size and shape and larger than oviposition holes, i.e., feeding cavity (Kanaujia and Levinson, 1981)]. The number and location of each type of weevil damage were recorded.

To investigate the mechanism behind females laying more eggs on larger kernels, individual females were exposed to either category two or four wheat kernels in a Lab-Tek two-well slide chamber (Nalge Nunc Int., Rochester, NY) with a floor area of 4.2 cm^2 in each chamber. A kernel was placed in each chamber, a piece of filter paper was inserted between the two chambers, an individual female was added to each chamber, and the chambers were covered. The arenas were placed in an incubator at 25°C and 70% RH, under infrared light. The weevils were videotaped for 6 h using a black-and-white CCD camera and time-lapse S-VHS recorder. The videotapes were reviewed to determine the time spent on and off the kernel, time until first visit to seed, time until initiate chewing a hole, time and duration of chewing and oviposition bouts, and number of visits.

The fitness consequences of kernel size and number of eggs laid were measured by holding wheat kernels and determining how many adult progeny emerged from them. Progeny sex was determined based on morphological characters (Halstead, 1963) and size was determined by measuring elytra length. The elytra were removed from each beetle and photographed with a digital camera, and the length of each elytra image was measured

using the measurement tool in Scion Image (Scion Corp., Frederick, MD). The average for each beetle's pair of elytra was used for analysis.

Analysis of variance or general linear models procedures with post hoc Tukey's multiple-range tests or SNK tests and paired t tests were performed using Systat version 9 for Windows (SPSS Inc., Chicago). Contingency table and goodness-of-fit analyses using log-likelihood ratio tests were performed using methods described by Zar (1999). Survival analysis was used to test for differences in latency until first visit to seed and initiation of oviposition. Survival analysis is appropriate for these types of observational experiments because they tend to have nonnormal distributions and some of the data are censored (i.e., the initiation times are only known to be longer than a certain cutoff time) (Kalbfleisch and Prentice, 1980). The log-rank test, to determine if survival functions are the same between treatments, was performed using Systat software. A significance level of $P < 0.05$ was used for comparisons, but Bonferonni corrections were used when multiple pairwise comparisons were performed. Data are typically presented as mean $\pm$ standard error of the mean.

RESULTS

Influence of Seed Size on Exploitation by Female *S. oryzae*

The characteristics of the seeds in the different size categories are presented in Table I. As expected, kernel weight, length, and width all increased with size category. Two other seed quality parameters, percentage moisture and protein content, were relatively stable across categories, but kernel hardness decreased with kernel size.

There was an influence of kernel size on how wheat was exploited by females (ANOVA; $F = 11.59$, df = 4, 195, $P < 0.001$) (Fig. 1). The number

Table I. Characterization of the Different Size Categories of Wheat Kernels[a]

	Size category				
	1	2	3	4	5
Weight (mg)	16.5 ± 2.7	16.8 ± 2.4	25.1 ± 3.0	34.0 ± 3.0	42.0 ± 3.0
Length (mm)	5.0 ± 0.1	5.2 ± 0.0	5.5 ± 0.1	5.8 ± 0.0	6.1 ± 0.0
Width (mm)	1.7 ± 0.0	2.2 ± 0.0	2.5 ± 0.0	2.8 ± 0.0	3.0 ± 0.0
Moisture (%)	14.3	14.4	14.4	14.4	14.6
Protein content (%)[b]	12.5	11.2	11.0	11	11.3
Hardness index	74.8 ± 1.3	74.3 ± 1.3	64.8 ± 1.2	58.2 ± 1.2	56.3 ± 0.9

[a]Data presented as mean $\pm$ standard error of the mean, except for moisture and protein content, which are based on the whole sample.
[b]Protein content adjusted to a standard of 14% moisture.

Seed size category
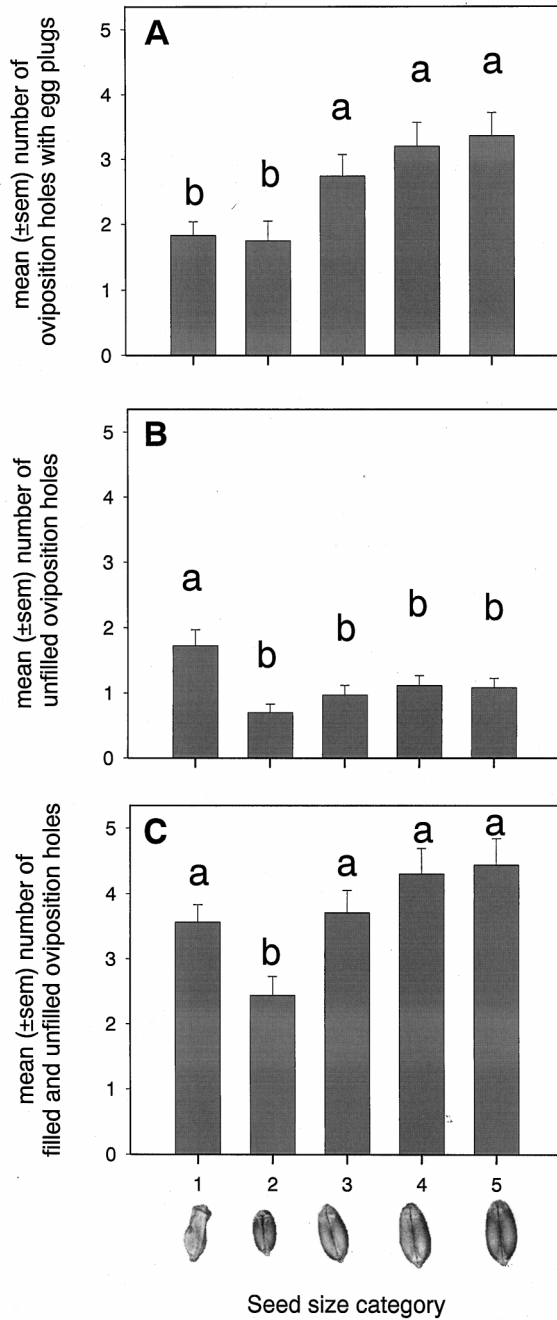
of eggs deposited into a wheat kernel was greater in the three largest kernel sizes compared to the shriveled and plump kernels less than 20 mg. The number of oviposition holes chewed by females in which they did not deposit an egg was also influenced by kernel size ($F = 10.17$, df = 4, 195, $P < 0.001$); more oviposition holes were present in the shriveled kernels than in any of the other categories. When oviposition holes with and without egg plugs were combined there was still a difference among size categories ($F = 10.68$, df = 4, 195, $P < 0.001$), but only the smallest whole kernels (category 2) had significantly fewer chewed holes. This indicates that weevils were chewing the same number of holes in the small shriveled wheat kernels as in the larger kernel sizes but were less likely to deposit eggs in the holes. There was no influence of seed size on the number of feeding holes in kernels ($F = 0.68$, df = 4, 195, $P = 0.609$).

There was variation among individuals in the average number of eggs laid in small (category 2) seeds ($F = 1.90$, df = 39, 78, $P = 0.008$) (Fig. 2A). Most individuals laid more eggs in larger kernels than in category 2 kernels; the average number of egg plugs in category 3 kernels was greater than or equal to that in category 2 kernels for 37 of the 40 individuals tested. To some extent, individual variation in exploitation of small seeds is explained by variation in female fecundity; there was a positive slope to the correlation between the number of eggs laid by a female weevil in category 2 kernels and the number laid by the same female in other, larger-sized kernel categories (Figs. 2C and D). However, the number of eggs laid in category 2 kernels explained less of the variation in number of eggs laid in category 4 and 5 kernels than it did for category 3 kernels (most similar in size to category 2). There was a poor correlation between the number of eggs laid in shriveled and that laid in plump kernels (Fig. 2B).

The tendency to lay more eggs in larger kernels may result from a tendency for females to take longer to accept smaller kernels. Females took longer to vist (Fig. 3A) (log-rank test; $\chi^2 = 8.544$, df = 1, $P = 0.003$) and longer to initiate oviposition (Fig. 3B) ($\chi^2 = 18.772$, df = 1, $P < 0.001$) on smaller wheat kernels than on larger kernels. The time for females to complete the process of oviposition and the number of times that they visited the kernel did not differ between kernel sizes, but they spent more time on the larger kernel and had a higher probability of ovipositing (Table II).

Fig. 1. The mean ($\pm$SE) number of oviposition holes with egg plugs (A), oviposition holes without egg plugs (B), and combined oviposition holes with and without egg plugs (C) created by female *Sitophilus oryzae*. Seed size categories are category 1 (shriveled kernels), category 2 (plump (unshriveled) kernels, <20 mg), category 3 (between 20 and 30 mg), category 4 (between 30 and 40 mg), and category 5 (>40 mg). Bars with the same lowercase letter represent means that are not significantly different (ANOVA and Tukey's multiple-range test; $P > 0.05$).
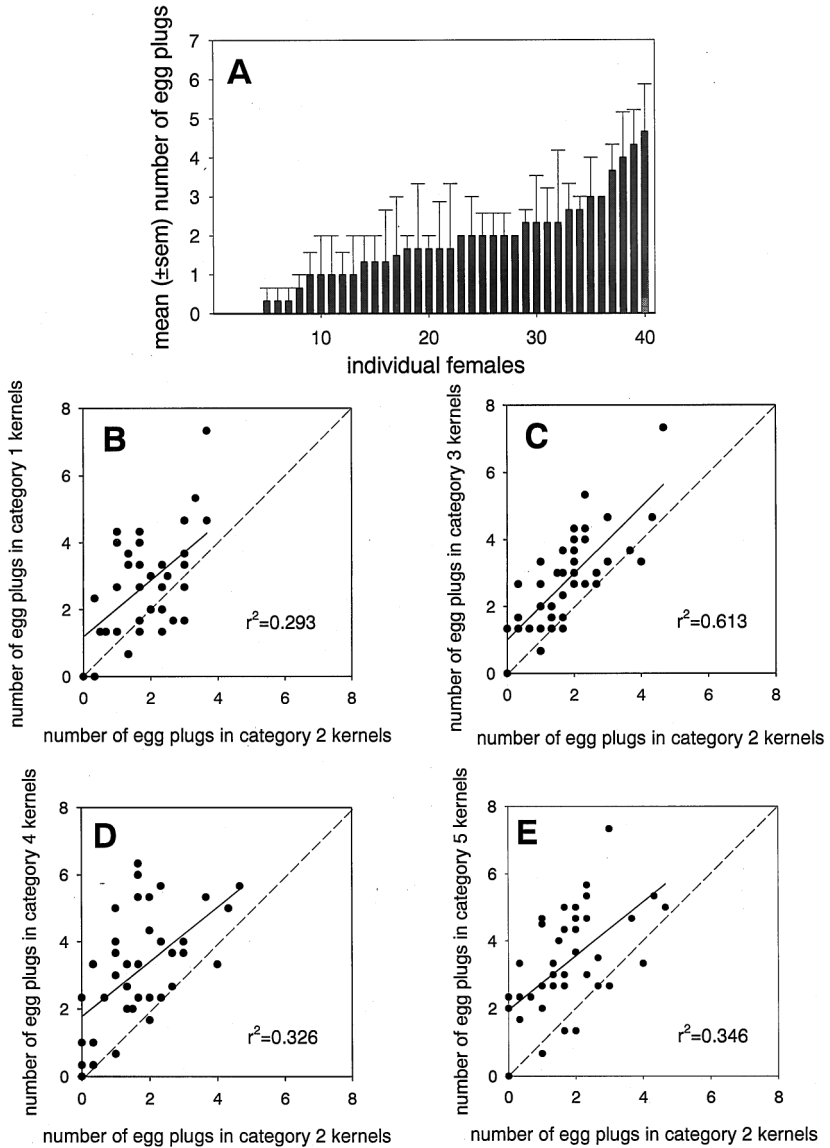
Fig. 2. The mean (±SE) number of oviposition holes with egg plugs laid by individual female *S. oryzae* in category 2 wheat kernels (<20 mg) (A) and the relationship between the number of egg plugs laid by individuals in category 2 kernels and the number laid by the same individuals in (B) category 1 (shriveled), (C) category 3 (between 20 and 30 mg), (D) category 4 (between 30 and 40 mg), and (E) category 5 (>40 mg) wheat kernels. In B–E, the solid line represents the correlation between the numbers of egg plugs in both size categories and the dashed line represents a reference line showing the one-to-one relationship between the numbers of egg plugs in both size categories.
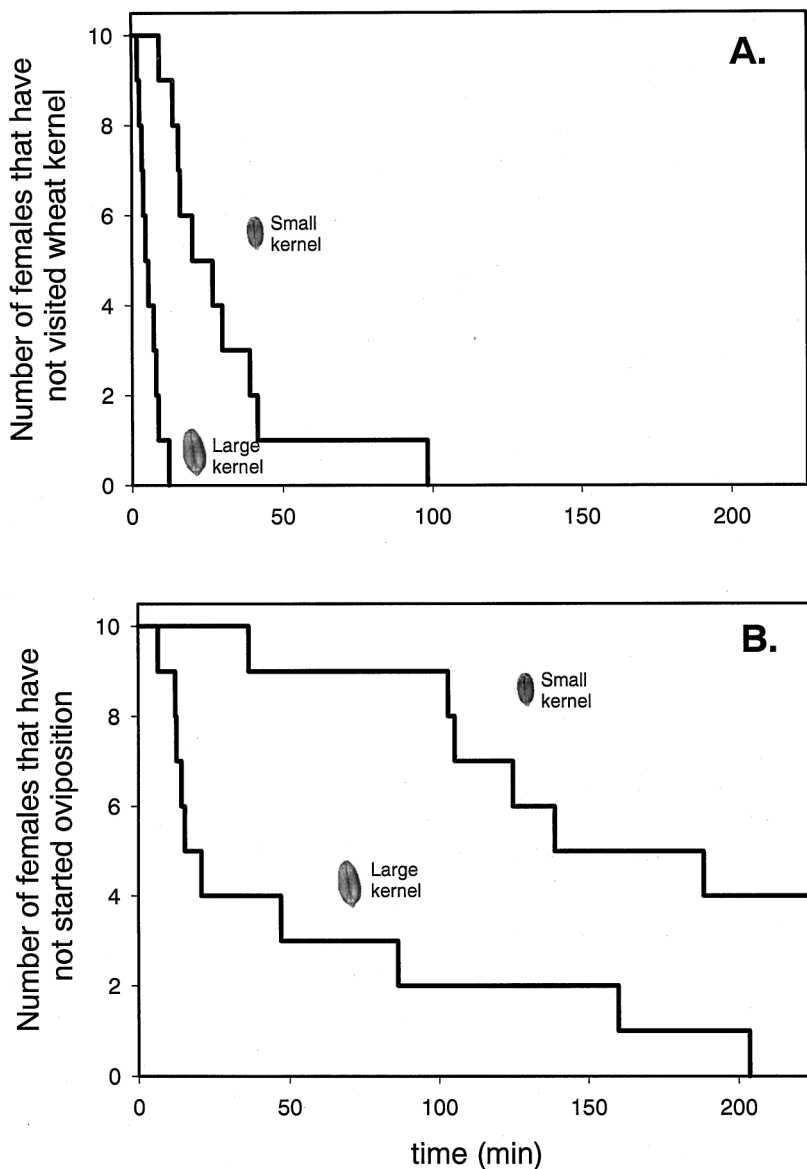
Fig. 3. Survival functions for the time until individual female *Sitophilus oryzae* initiate visits to a wheat kernel (A) and initiate chewing an oviposition hole (B). Females were held with only one kernel that was either category 2 (<20 mg) or category 4 (between 30 and 40 mg).

Table II. Differences in Seed Exploitation by Female *S. oryzae* Between Small (Category 2; <20 mg) and Large (Category 4; Between 30 and 40 mg) Kernels of Wheat

Behavioral parameter	Small wheat kernel[a]	Large wheat kernel[a]	Statistics
Visits until oviposition	4.7 ± 1.3 (6)	2.6 ± 0.8 (10)	$t = -0.908$, df $= 5$, $P = 0.406$[b]
Duration of chewing bout	80.2 ± 6.5 (6)	84.3 ± 11.0 (10)	$t = 1.535$, df $= 5$, $P = 0.185$
Duration of oviposition bout	4.6 ± 0.4 (6)	5.3 ± 0.9 (10)	$t = 1.520$, df $= 5$, $P = 0.189$
Total number of visits	15.4 ± 2.8 (10)	15.3 ± 2.5 (10)	$t = -0.026$, df $= 9$, $P = 0.980$
Total time on kernel	190.4 ± 27.0 (10)	303.9 ± 16.5 (10)	$t = 3.064$, df $= 9$, $P = 0.013$
Probability of oviposition	1.0	0.6	
Conditional probability of second oviposition	0.5	0.33	
Probability of clutch size of two	0.2	0.17	

[a]Data presented as mean ± SE (n).
[b]Paired-samples t test.

Multiple ovipositions resulted from females leaving the kernel after one oviposition and then returning to lay additional eggs (self-superparasitism) or females laying more than one egg before leaving the seed (clutch size greater than one). The proportion of females that laid two eggs per visit was similar for the large (0.20) and small (0.17) kernels.

Fitness Consequences of Oviposition Decisions

There was an effect of kernel size category on probability of emergence (log-likelihood ratio test for contingency table; $G = 13.3$, df $= 4$, $P < 0.025$), but this was due to lower emergence from shriveled kernels (Table III). When the shriveled category 1 kernels were excluded from analysis there was no significant difference among the remaining categories ($G = 2.8$, df $= 3$, $P > 0.05$). The conditional probability of a second progeny emerging from a kernel did not increase with kernel size ($G = 6.3$, df $= 4$, $P > 0.05$). Despite variation in the number of eggs deposited per kernel, the proportion of eggs surviving to the adult stage was relatively constant across kernel size (Table III).

Analysis of the progeny indicated that sex ratio was not affected by kernel size but that progeny size increased with increasing kernel size (Table III). Sex ratio did not differ among the kernel sizes (log-likelihood ratio test for contingency table; $G = 1.4$, df $= 4$, $P > 0.05$). The combinations of males and females emerging from kernels producing two progeny

Table III. Fitness Parameters Associated with Oviposition by *Sitophilus oryzae* in Different Categories of Wheat Kernels

Wheat kernel category[a]	n^b	Probability of emergence[c]	Conditional probability of second progeny	Sex ratio (M:F)	No. emerging/ No. egg plugs	n^d	Progeny elytra length (mm)[e]
1	105	0.69	0.06	1.09	0.35 ± 0.03	78	$1.72 \pm 0.014a$
2	98	0.79	0.03	0.85	0.36 ± 0.03	78	$1.77 \pm 0.014b$
3	103	0.84	0.07	0.84	0.30 ± 0.02	91	$1.84 \pm 0.011c$
4	108	0.83	0.09	0.74	0.26 ± 0.02	97	$1.89 \pm 0.009d$
5	109	0.88	0.125	0.83	0.29 ± 0.02	109	$1.91 \pm 0.009d$

[a]Category 1 (shriveled kernels); category 2 (unshriveled kernels, <20 mg); category 3 (between 20 and 30 mg); category 4 (between 30 and 40 mg); and category 5 (>40 mg).
[b]Number of kernels used to calculate emergence from kernels.
[c]Probability of one or more progeny emerging from a kernel with at least one egg plug.
[d]Number of individuals measured to determine progeny size.
[e]Average length $\pm$ SE of elytra from progeny. Means in column followed by the same letter are not significantly different (Tukey's multiple-range test, $P > 0.05$).

(8 male–male, 7 female–female, and 16 male–female) did not differ from predictions ($G = 0.126$, df $= 2$, $P > 0.05$). Progeny body size, as measured by elytra length, increased with increasing kernel size (general linear models analysis; $F = 52.39$, df $= 4, 448$, $P < 0.001$). There was a difference between the sexes in elytra length when progeny from the different kernel sizes were combined; females were larger (1.854 ± 0.008 mm) than males (1.816 ± 0.01 mm) (*t* test; df $= 178$; $P = 0.001$).

The influence of the number of eggs deposited within a kernel on the probability of emergence and progeny size was investigated. When the category 3–5 wheat kernels were combined, the proportion of kernels with at least one weevil emerging was 0.83 for one egg plug, 0.76 for two egg plugs, 0.88 for three egg plugs, 0.87 for four egg plugs, 0.80 for five egg plugs, 0.94 for six egg plugs, and 0.89 for seven or more egg plugs. There was a significant difference in proportion emerging among egg plug number (log-likelihood ratio test for contigency table; $G = 215.5$, df $= 6$, $P < 0.001$), but there was not a trend for the probability of emergence to increase with the number of egg plugs. There was no significant difference in the probability of two progeny emerging from a kernel with different numbers of egg plugs ($G = 7.4$, df $= 5$, $P > 0.05$): 0.1, 0.04, 0.14, 0.04, 0.11, and 0.11 for two, three, four, five, six, and seven or more egg plugs, respectively. The progeny size from kernels with only one adult emerging increased with the number of egg plugs (general linear models analysis; $F = 2.97$, df $= 6,239$, $P = 0.0082$): 1.844 ± 0.019, 1.843 ± 0.016, 1.867 ± 0.013, 1.886 ± 0.013; 1.908 ± 0.013, 1.907 ± 0.017, 1.919 ± 0.021 for two, three, four, five, six, and seven or more egg plugs, respectively. A SNK test indicated that

only one and two egg plugs and seven or more egg plugs were significantly different from each other.

DISCUSSION

Optimality models generally predict that larger clutches will be laid in higher-quality hosts because they can support more progeny (Godfray *et al.*, 1991). Female *S. oryzae* were more likely to lay multiple eggs in large kernels [i.e., significantly more eggs were laid in kernels ≥20 mg (category 3–5 kernels)]. Changes in the number of eggs laid by *S. oryzae* in different seed sizes appear to be consistent with the hypothesis that females assess seed quality and adjust the number of eggs laid. However, multiple eggs per seed appear to be due primarily to an increase in the visits resulting in oviposition, not an increase in the number of eggs laid per visit, and the additional eggs laid do not correlate well with a higher number of progeny being produced from the seed. Observations of females exposed to single seeds suggest that they typically lay one egg per visit, with two eggs laid in approximately 20% of visits. Thus, most cases of two or more eggs per seed probably result from multiple clutches of one egg (self-superparasitism). Clutch size did not increase with kernel size, but the level of self-superparasitism did increase. At most two progeny were observed to emerge from an infested kernel. Seven or more eggs per seed did result in larger progeny, perhaps due to nutritional benefits of cannibalism or competition favoring larger individuals, but in general the fitness benefits of self-superparasitism were limited. Confinement of females with kernels probably contributed to higher levels of oviposition per seed then are typical. However, differences in number of egg plugs among seed categories do reflect differences in female response to seeds and the fitness consequences of egg number and seed size should be independent of the experimental protocol. Additional choice experiments are needed to determine how the behavioral mechanisms determined in this study impact the distribution of eggs among multiple kernels.

Previous studies have indicated that *Sitophilus* spp. prefer larger kernels but have typically looked at the distribution of eggs among seeds when exposed to multiple females (e.g., Ewer, 1945; Segrove, 1951; Pederson, 1979; Stejskal and Kučerová, 1996). Interpretation of these studies is complicated by the inability to assess the relative importance of clutch size and superparasitism. Stejskal and Kučerová (1996) found that the distribution of *S. granarius* eggs was always aggregated but that egg aggregation decreased with increasing number of wheat kernels. They also reported that more progeny emerged when weevils were held on small kernels than on large kernels, probably due to fewer eggs per seed in the smaller kernels.

Pederson (1979) reported that in a sample of *S. oryzae*-infested wheat, 92% of kernels contained one egg and 7.8% contained two eggs, but as the seed moisture increased the number of kernels with two eggs increased and the number with one egg decreased. This suggests that moisture content may influence clutch size. Seed moisture was the same among the seed categories in this experiment but may also be a measure of seed quality for *S. oryzae*. Seed length and width and seed hardness also varied among kernel categories, but the mechanism used by weevils to evaluate host quality as correlated with host size is not known. Volatile and visual cues may be important in initial seed acceptance, because differences in seed visitation time between category 2 and category 4 kernels were observed. Seeds produce volatile and gustatory cues that have been shown to influence *Sitophilus* spp. behavior (Kanaujia and Levinson, 1981).

There were fitness benefits and costs to laying eggs into seeds of different sizes. The probability of an adult emerging from a seed was lowest for small shriveled kernels but did not differ among the other categories. The conditional probability of a second adult emerging from a seed was not different among the tested seed categories. The biggest fitness advantage to ovipositing into larger kernels was an increase in progeny size. Larger individuals typically have higher fitness than smaller individuals. Ungsunatwiwat and Mills (1985) found that *S. oryzae* elytra length differed among seed types on which the progeny were reared and that seed characteristics had more of an impact on progeny size than did parent size. The total number of eggs in the ovaries of virgin female *S. granarius* has been reported to increase with the female weight (although interpreting this is difficult because eggs contribute to an individual's weight) and heavier individuals tended to have a higher oviposition rate (Richards, 1947). Richards also reported that male size did not impact on female egg number or oviposition rate, but larger *S. oryzae* males do appear to have an advantage over smaller males in mating opportunities (Campbell, unpublished data).

Povey and Sibly (1992) reported that *S. oryzae* did not reduce egg laying under poor conditions and increase egg laying when condition improve (i.e., exhibit oviposition plasticity). This may be because *S. oryzae* females are unable to use cues indicating the presence of poor-quality grain or are physiologically unable to adjust the rate of egg laying. The results presented here indicate that, at least in the short term, *S. oryzae* is able to reduce egg laying in the presence of lower-quality resources (i.e., lay fewer eggs when held with only small seeds), and this results in part from a longer acceptance time for poorer quality seeds. Some of this size preference may be learned behavior because previous exposure to only small kernels resulted in an increase in the number of eggs laid in category 2 kernels (Campbell, unpublished data). These results suggests that *S. oryzae* may have some flexibility

in its oviposition behavior and further research is needed to determine what other factors influence *S. oryzae* acceptance of seeds.

The results presented here are also consistent with previous observations that female *S. oryzae* do not discriminate between parasitized and unparasitized hosts (Giga and Smith, 1985; Smith and Lessells, 1985). In contrast to *Sitophilus*, many bruchid seed parasites have a marking pheromone and females avoid ovipositing in previously parasitized hosts. This leads to an even distribution of eggs among seeds that is frequently reported for bruchids (Mitchell, 1975) but not for *Sitophilus* (e.g., Smith and Lessells, 1985; Urrelo and Wright, 1989). Legg *et al.* (1987) suggested that weevil density, oviposition/feeding period, host genotype, and kernel density could influence egg distribution. Superparasitism can be costly for *S. oryzae* if time, eggs, or resources are limited. Povey and Sibley (1992) speculated that because bruchid beetles such as *Callosobruchus maculatus* are more egg and time limited than *Sitophilus* spp.. *S. oryzae* females in the laboratory lay eggs over a long period of time (Richards, 1947), mate frequently throughout their life (Campbell, unpublished data), and frequently occur in bulk stored grain where they are unlikely to be resource limited. Therefore, females may not have strong selection pressure to host discriminate. It is also possible that *Sitophilus* females have other behavioral or physiological traits to reduce the chance of superparasitism (e.g., increased activity following oviposition, decreased response to oviposition cues, delay in egg maturation). For example, *S. granarius* do not apparently detect the presence of egg plugs on a seed but lay few eggs in wheat kernels containing late-instar larvae (Ewer, 1945) and prefer clean grain to grain exposed to males or virgin females (Stubbs and Abood, 1983).

The observation that superparasitism occurs does not necessarily mean that the female is unable to discriminate between a parasitized and unparasitized host (Salt, 1961; van Lentern, 1981), because there are situations where superparasitism is favored by natural selection (van Alphen and Nell, 1982; Parker and Courtney, 1984; Charnov and Skinner, 1985; Waage and Godfray, 1985). In contrast, self-superparasitism, when a female attacks a host that she herself has previously attacked, is nearly always costly in time and eggs (Waage, 1986) and can increase the risk of host damage and reduce the first egg clutch survival (van Lenteren, 1981). For self-superparasitism to be adaptive, the female's assessment of the environment has to change after the first visit so that laying additional eggs becomes adaptive (Waage, 1986). It is possible that confining females with single seeds even for relatively short times changes their perception of the environment. The fitness costs of self-superparasitism appear to be high for *S. oryzae*, but clearly, some of this cost is a result of the experimental protocol used. As the probability of reencountering a particular parasitized seed is reduced, so is the probability

of self-superparasitism. Additional changes in the seed over time after initial parasitism may also influence the probability of females exploiting the seed again.

The link between individual behavior and population dynamics can be important for pest management (Smith, 1986). The costs and benefits of different oviposition decisions will influence *S. oryzae* behavior through the process of natural selection. Understanding these relationships will improve our understanding of pest behavior and ecology and, ultimately, our ability to manage these important grain pests. For example, variation in seed quality on oviposition decisions may contribute to differences in varietal resistance in *Sitophilus* parasitization (e.g., Singh *et al.*, 1974; Gomez *et al.*, 1982; Urrelo and Wright, 1989). Urrelo and Wright (1989) investigated the host selection mechanisms of *S. zeamais* in corn and found that the number of egg plugs was influenced by the interaction between corn variety susceptibility rating and kernel size. The impact of oviposition decisions on *S. oryzae* intraspecific interactions, spatial distribution, and population dynamics is potentially important and needs further investigation. Results presented here indicate that females make decisions regarding seed quality and that there are costs and benefits to these decisions. These costs and benefits to individuals under more natural conditions in food storage landscapes need to be addressed.

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