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Patch Exploitation by female Red Flour Beetles, *Tribolium castaneum*

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Abstract

The red flour beetle, *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) has had a long association with human stored food and can be a major pest in anthropogenic structures used for the processing and storage of grain-based products. Anthropogenic structures are fragmented landscapes characterized by spatially and temporally patchy resources. Here we investigate the ability of female *T. castaneum* to evaluate the quality of small patches of food and to adjust the number of eggs they lay per patch (i.e., clutch size) to maximize fitness gains. In multiple choice, paired choice and no choice experiments females tended to lay more eggs in larger amounts of flour. The number of eggs that they lay in a patch of flour was consistent with that predicted to optimize production of adults from that patch (i.e., the 'Lack' clutch size). Progeny size was only significantly impacted in the smallest patch sizes.

Keywords: stored-products, behavior, clutch size, oviposition

Introduction

After encountering a patch of resource, female insects need to decide if the resource is suitable for oviposition and if so how many eggs to lay (Charnov and Skinner, 1985). Lack (1947) originally proposed the hypothesis that a female should lay the number of eggs that maximizes her gain in fitness (e.g., number of progeny produced) from the whole clutch of eggs. The Lack hypothesis assumes that maximizing lifetime fitness is equivalent to maximizing the fitness of each egg clutch. The number of eggs conferring the maximum fitness for a clutch is often referred to as the Lack clutch size (Charnov and Skinner, 1985). The Lack clutch size is strongly influenced by resource quality and smaller clutches are predicted for lower quality resources. This hypothesis was originally developed for bird egg clutches, but has also been widely applied to insect clutch sizes, especially for parasitoids (Charnov and Skinner, 1985; Godfray et al., 1991).

The red flour beetle, *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) can be a major pest in anthropogenic structures used for the processing and storage of grain-based products (e.g., flour mills, warehouses, retail stores). This species has had a long association with human stored food and has been found in association with a wide range of commodities including grain, flour, peas, beans, cacao, nuts, dried fruits, and spices, but milled grain products such as flour appear to be their preferred food (Good, 1936). *Tribolium castaneum* may have originally occurred primarily in rotting logs and under tree bark feeding on plant and animal detritus, and on insect eggs and pupae (Sokoloff, 1974). These natural and

anthropogenic landscapes are characterized by spatially and temporally patchy resources. The ability of this species to find and colonize patches of food and to persist on small amounts of food that accumulate *in refugia* contributes to its pest status (Campbell and Hagstrum, 2002). However, most studies of *T. castaneum* oviposition have focused on behavior in relatively large amounts of food. Here we investigate the ability of female *T. castaneum* to evaluate the quality of small patches of food and adjust the number of eggs they lay per patch (i.e., clutch size) to maximize fitness gains in terms of number of adult progeny from a patch.

It has been proposed that *T. castaneum* is a primary colonist and is among the first species to find and exploit pristine resource patches and is perhaps one of the few stored-product pest species to colonize widely dispersed patches with rapidly depleted resources (Ziegler, 1976). *Tribolium* spp. are highly mobile within large patches of food such as grain or flour (Surtees, 1963, 1964; Hagstrum and Leach, 1972; Hagstrum, 1973) and readily disperse from patches of flour throughout the adult stage (Hagstrum and Gilbert, 1976; Lavie and Ritte, 1978; Naylor 1961; Ogden 1970; Ziegler, 1976, 1977). Most studies that measured movement between patches of food have restricted movement using artificial channels among food patches (Naylor, 1961; Lomnicki and Krawczyk, 1980; Ben-Shlomo et al., 1991). Campbell and Hagstrum (2002) found that when allowed to move freely among multiple patches, both males and females visited multiple patches, eggs were distributed among patches, and individuals were often observed outside of food patches.

Female *Tribolium* spp. adults are long lived and lay eggs more or less continuously over their life, but oviposition is influenced

by a variety of internal and external factors. Good (1936) and Howe (1962) found that female *T. castaneum* maintained high rates of oviposition for over 100 days at 25° C, sometimes laying eggs for over 300 days, and that they had an average life time fecundity of more than 300 eggs. Oviposition is, however, influenced by a range of environmental conditions such as temperature and relative humidity (Good, 1936; Park and Frank, 1948; Howe 1962), type of food material (Good, 1933), and crowding (Birch et al., 1951). The conditioning of flour by conspecifics strongly influences *T. castaneum* oviposition and dispersal, and it is reported that this species prefers flour that has not been previously exploited (Ziegler, 1976). A common characteristic of most of these studies is that the beetles were confined to the resource patch and were not allowed to choose oviposition substrates. Stanley and Grundmann (1965) showed that when *T. confusum* was presented with a choice of different flour depths, they laid more eggs in the deeper flour.

In this study, the ability of female *T. castaneum* to allocate eggs among patches that differ in quality was first assessed using multiple choice, paired choice, and no choice experiments. The quality parameter manipulated in this study is the amount of food material that is present in the patch. Then the fitness consequences (e.g., number of progeny produced, progeny size) of different oviposition decisions were evaluated by adding set numbers of eggs to different amounts of flour and measuring probability of survival to the adult stage, adult size, and sex ratio. From these data, optimal oviposition (i.e., Lack clutch size) decisions for a given amount of flour were evaluated and compared to the oviposition decisions actually made by females.

Materials and Methods

Oviposition behavior – choice experiments

Four choice experiment: How male and female pairs allocate time and eggs among patches containing different distributions of flour was measured using 42 cm x 32 cm trays (Steeelite, www.steelite.com) as arenas. The bottom of each tray was painted with white pigmented primer sealer (William Zinsser and Co., www.zinsser.com) containing fine grain sand to facilitate beetle traction. To confine insects, the sides of the tray were treated with Fluon (Northern Products Inc., Woonsocket RI) and the top of the sides had a band of Tangle-trap sticky compound (Tanglefoot Company, www.tanglefoot.com). A grid (2.5 cm by 2.5 cm squares, except in the corners of the tray where the shape was a triangle) was drawn on the bottom of the tray with pencil. Artificial refugia were created using two glass slides (7.6 cm by 2.5 cm, 0.96-1.06 mm thick) separated by two pieces of fiber gasket material (1.59 mm thick) placed along the short ends of the slides and held in place with clear tape. Flour (with 5% brewers yeast added and sieved through a 60 mesh [250 µm] sieve) was added to the space between the glass slides. These artificial refugia provided the beetles with shelter, food and oviposition substrate, while enabling us to observe beetles without disturbance and facilitating the removal of flour for egg detection. Four glass slide flour patches were placed in each arena near the corners and 2.5 cm from the edges. Three distributions of flour were compared: one patch with flour (0.40 g) and three without flour; four patches each with 0.10 g of flour; and four patches

with 0.01, 0.04, 0.10, and 0.25 g, respectively. The total amount of flour in the arena was the same for all treatments.

Beetles were obtained from a laboratory colony maintained on the same flour yeast mixture (hereafter just referred to as flour). They were sexed as pupae (Good, 1936) and held until at least one week after adult eclosion. Males and females were marked on the thorax with different colored nail polish and one virgin male and one virgin female were combined in a cup (with small amount of oatmeal) for three days prior to start of experiment. A male and female were added to each arena for one week. Trays were placed in a walk-in incubator at 23° C and 70% relative humidity with lights on continuously. All the treatments in a replicate were assigned to a shelf with the location of each tray on the shelf randomized. There were 10 replicates in two blocks of five replicates each. Each block used a different set of beetles. The location of the beetles was checked twice daily. At the end of the week, the flour patches were removed, sieved through a 50 mesh (297 µm) sieve and the number of eggs present in each patch was determined.

Paired choice experiment: Females were presented with two artificial refugia patches with flour as described above in inverted 150 mm petri dishes with Whatman #42 150mm filter paper in the lid. In all treatments one of the patches contained 0.10 g of flour and the other patch contained one of the following amounts of flour; 0.40, 0.20, 0.10, 0.04, 0.02, and 0.01 g. Slides were placed 4 cm apart on the filter paper within the petri dish. Twenty replicates of each treatment were performed in two blocks of 10 replicates. Two different sets of beetles were used for each block. Females were selected as pupae from a laboratory colony and held individually until adult eclosion. Females were marked with a small dot of nail polish on their thorax for identification and held with males until the start of the experiment (1-2 weeks). Individual females were added to each dish and held at 25°C for 48 hours. Females were then removed and the flour from the patches sieved and the number of eggs present counted.

Oviposition behavior – no choice experiment

Females were presented with one artificial refugium, created as described above, placed in the center of an inverted 90 mm Petri dish with Whatman #1 90 mm filter paper in the lid. Twenty replicates, performed in two blocks of 10 replicates, of the following amounts of flour per patch were run: 0.0, 0.005, 0.01, 0.02, 0.04, 0.08, 0.10, 0.20, 0.40, and 1.0 g. Females were selected as pupae from a laboratory colony and held individually until adult eclosion. Females were marked with a small dot of nail polish on their thorax for identification and held with males until the start of the experiment (1-2 weeks). Individual females were added to each dish and held for 48 hours. Females were then removed and the flour from the patches sieved and number of eggs present counted.

Fitness consequences of oviposition

The influence of egg number and patch size on offspring survival to adulthood and adult size was tested by adding 1, 2, 4, 8 or 12 eggs to different amounts of flour. The following amounts of flour were placed in 29.6 ml plastic cups: 0.005, 0.01, 0.02, 0.04, 0.08, 0.10, 0.20, 0.40, 0.80 and 1.00 g of flour/yeast mixture. Then the eggs were added to the flour, the cups were covered, and stored

in an incubator at 25° C. Eggs used in this experiment were less than 24 hours old. Five replicates were performed of each egg number/amount of flour combination. The cups were incubated undisturbed for 5 weeks. Thereafter, any adults present were removed on a weekly basis until no more living adults, pupae or larvae were observed in the cups. After collection, the sex and size of all adult progeny was determined. Adult size was determined by removing both elytra from each beetle, taking a digital photo and measuring the length of each elytron using Scion Image v. beta 4.0.2 software (Scion Corporation, www.scioncorp.com). The average of the two elytra lengths was used for analysis.

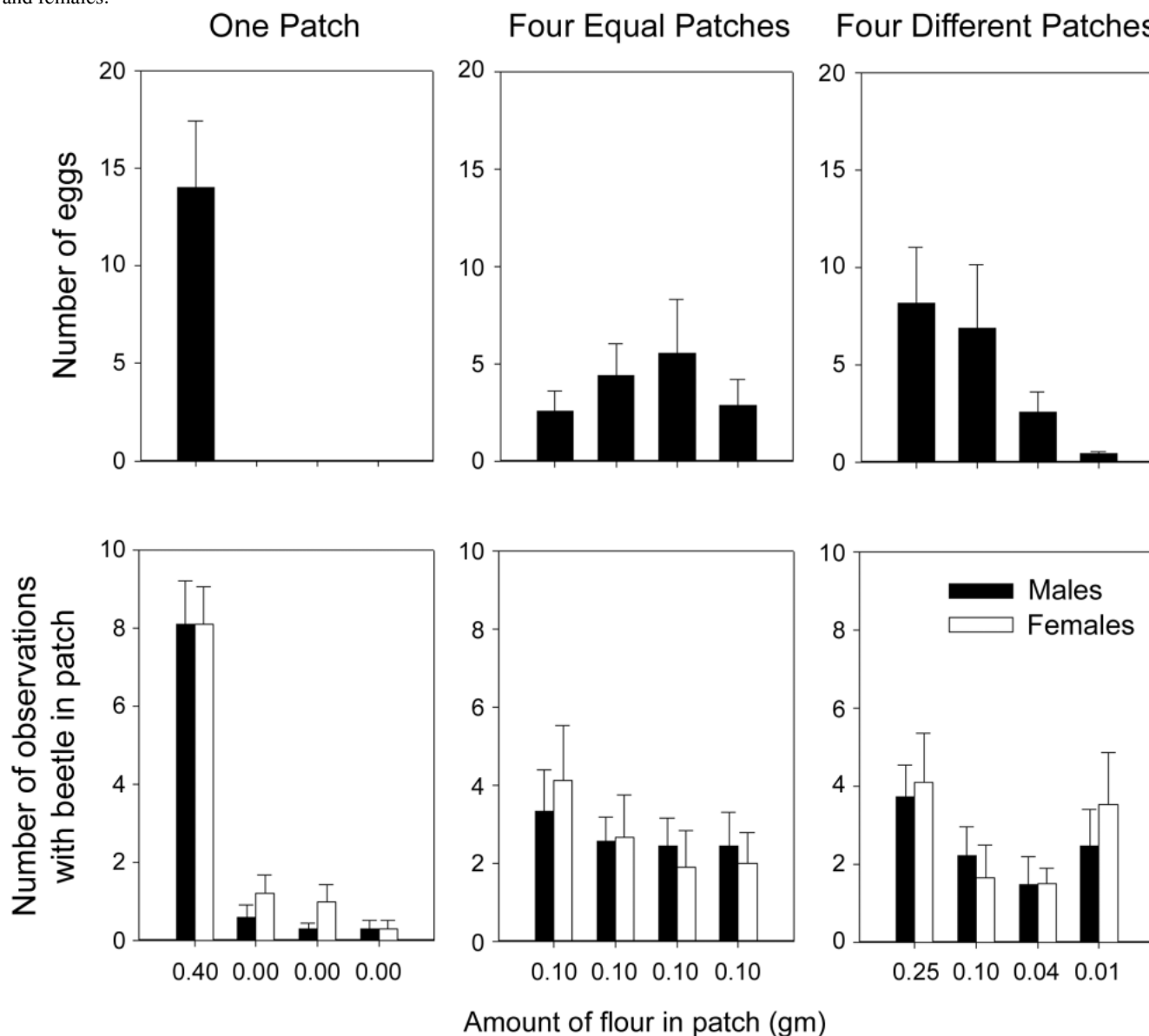
The optimal number of eggs to lay in a flour patch of a given size was calculated using the data collected above by first estimating the probability of producing x adults from a given amount of flour. To determine this probability, all of the egg number treatments for a given amount of flour were combined and the

number of replicates with at least x adults emerging was divided by the total number of replicates with at least that number of eggs added (clutch size c , ranging from 1-12 eggs). Then a function $f(c)$ to describe the probability of producing increasing numbers of adults for each flour patch size based, in all cases but one on the sigmoid model, was fit using TableCurve 2D v. 5 (Systat Software, www.systat.com). Finally, the fitness gain per patch was calculated as $c*f(c)$ for each clutch size (c) up to 12 and the clutch size with the highest fitness gain per patch was selected as the optimal number of eggs (i.e., the Lack clutch size).

Statistical Analysis

Contingency table analysis using the log-likelihood ratio test was used for all frequency of occurrence data such as egg distribution among patches (Zar, 1999). General linear models analysis of variance procedures for unbalanced data and Tukey's

Figure 1. The effect of distribution of flour among four artificial refugia [four different amounts of flour (0.25, 0.10, 0.04, and 0.01 gm, respectively); four equal amounts of flour (0.10 gm in each refugia); one refugia with 0.40 gm flour] on *Tribolium castaneum* oviposition and on occupation of different refugia by males and females.



multiple range tests were performed using SAS system for Windows v. 8 software (SAS Institute, Cary NC). Correlation analysis using Pearson correlation coefficient was performed using Systat v. 8 (Systat Software, Richmond CA).

Results

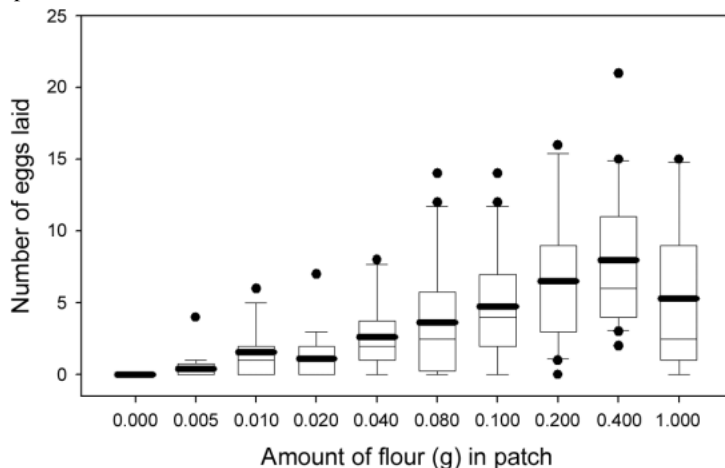
Oviposition behavior – choice experiments

Four choice experiment: There were differences in egg distribution among patches among the flour distribution treatments (Fig. 1), but no difference in the total number of eggs laid among the treatments (General Linear Models procedure: $F=0.42$, $d.f.=2, 25$, $P=0.6634$). The average total number of eggs per arena for the combined treatments was 16.3 ± 2.6 eggs ($n=28$). In the treatment with only one patch containing flour, no eggs were found in any of the patches without flour. When the treatment with four patches each with 0.10 g of flour and the treatment with four patches with 0.01, 0.04, 0.10, or 0.25 g of flour were compared, the distribution of eggs among flour patches was different (Log-likelihood ratio test for contingency tables: $G=78.5$, $\chi^2_{0.05,3}=7.8$, $P<0.001$). Replicates with no oviposition were excluded from analysis (one replicate for the four equal patch and one replicate from the four different patch treatments).

The three treatments differed in the distribution of male ($G = 59.4$, $\chi^2_{0.05,6} = 12.6$, $P<0.001$) and female ($G = 80.2$, $\chi^2_{0.05,6} = 12.6$, $P<0.001$) observations in patches (Fig. 1). Pair-wise comparisons indicate that this was due to differences between the treatment with only one patch containing flour and the other two treatments with some flour in all patches ($P<0.001$). Treatments with the flour equally and unequally distributed among the four patches did not differ in either male ($G = 7.1$, $\chi^2_{0.05,3} = 7.8$, $P>0.05$) or female ($G = 2.7$, $\chi^2_{0.05,3} = 7.8$, $P>0.05$) observations.

Paired choice experiment: Females laid significantly more eggs in the larger patch in the combinations with greater than 0.06 g difference between the two patches (Table 1). Only individuals that laid at least one egg were included in the analysis. When presented with two patches with the same amount of flour, on average females laid a similar number of eggs in both patches. The greater the difference in amount of flour between the two patches the greater

Figure 2. The number of eggs laid by female *Tribolium castaneum* in different amounts of flour in a no choice experiment. Boxes represent 25th to 75th percentile of the data, whiskers represent the 10th and 90th percentiles, circles represent outliers, thin lines through box represent the median and thick lines represent the mean.



the difference in the number of eggs laid. In the treatments with the most extreme differences between patch sizes, most individuals did not lay any eggs in the smaller patch. For example, 75% (12/16 individuals), for 0.01 g and 0.1 g comparison, and 100% (0/8 individuals), for 0.4 g and 0.1 g comparison, of individuals did not lay any eggs in the smaller patch.

Oviposition behavior – no choice experiment

When females were presented with a single patch of flour, the average number of eggs laid tended to increase with increasing patch size up until about 0.2 g of flour (Fig. 2). There was however considerable individual variation in the number of eggs laid. The relationship between the average number of eggs laid and the amount of flour present in artificial refugia was best explained using an exponential rise to a maximum equation ($y=6.716(1-e^{-12.145x})$; $r^2=0.925$)

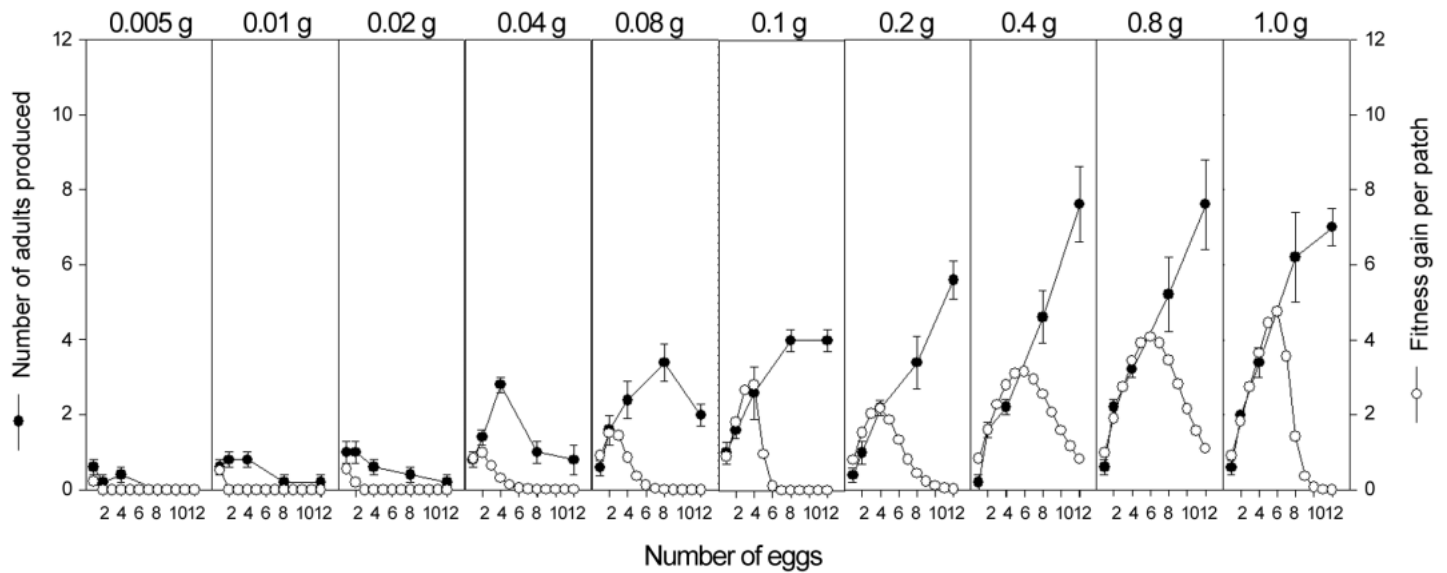
Fitness consequences of oviposition

In general, the number of adults that could be produced

Table 1. Comparison of the number of eggs laid in each of two patches containing different amounts of flour/yeast mixture by female *Tribolium castaneum* when presented with a paired choice.

Amount of flour (g) in patch 1	Number of eggs laid in patch 1 (mean±sem)	Amount of flour (g) in patch 2	Number of eggs laid in patch 2 (mean±sem)	Individuals that laid eggs (n)	t-statistic (paired two-tailed t-test)	P-value
0.01	0.4±0.2	0.1	6.1±1.2	16	4.55	0.0004
0.02	1.1±0.3	0.1	5.2±1.2	18	3.47	0.0029
0.04	1.6±0.8	0.1	3.2±0.9	9	1.4	0.199
0.1	2.4±0.8	0.1	1.4±0.3	12	1.34	0.2087
0.2	7.9±1.3	0.1	3.3±0.9	18	2.98	0.0084
0.4	7.5±1.9	0.1	0.7±0.5	8	3.47	0.0104

Figure 3. Number of adult progeny produced and the fitness gain to the mother per patch for a clutch of that size from different combinations of amount of flour and number of eggs.



increased with the amount of flour, but the relationship between number of eggs and adult production varied with amount of flour (Fig. 3). For flour amounts of 0.2 g and greater, the number of progeny that survived to adulthood increased with number of eggs. The increase in adult production was not proportional to the number of eggs deposited for any of the tested amounts of flour.

The fitness gains (measured as adult production) per patch of adding additional eggs to given amounts of flour is plotted in Fig. 3. At most flour amounts there was a clear peak in the fitness gains of laying increasing numbers of eggs. In smaller amounts of flour there was little or no increase in adult production with additional eggs deposited. Overall the average number of eggs laid by females in a patch of flour (as determined in the no-choice experiment) corresponded with the predicted clutch size for a patch of that size derived from the results of this experiment (Fig. 4). The Pearson correlation coefficient for this relationship was $R^2=0.910$.

A general linear models procedure indicated a significant difference in progeny size (i.e., elytra length) ($F=2.99$, $df=49$, 479, $P<0.0001$) with the class variables amount of flour and number of eggs. The class variable amount of flour was significant ($F = 9.94$, $df = 9$, $P<0.0001$), but the class variable number of eggs was not significant ($F = 1.80$, $df = 6$, $P=0.0973$) nor was the interaction between the two class variables ($F = 1.36$, $df = 24$, $P = 0.0883$). Because amount of flour was the only significant effect, elytra length was compared across amounts of flour using Tukey's multiple range test (SAS Institute, date) (Table 2). Elytra lengths of beetles from 0.005 g and 0.01 g of flour were shorter than from all other amounts of flour. The sex ratio of progeny was close to 0.5 for all amounts of flour, except at low amounts of flour where low progeny production reduced the accuracy of the estimate (Table 2).

Discussion

Female red flour beetles evaluate the size of a food patch

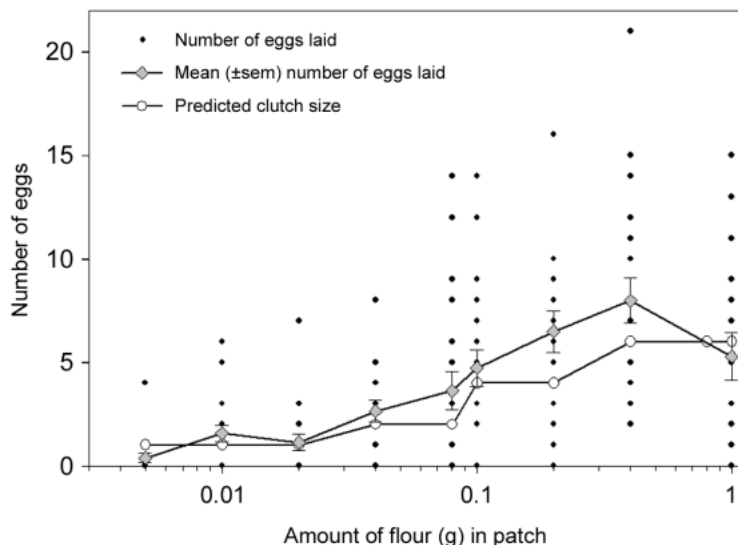
and adjust the number of eggs that they lay in that patch in a way that is consistent with that predicted to optimize production of adults from that patch. Even relatively small differences in amount of flour generated significant differences in the average number of eggs laid. In multiple choice, paired choice and no choice experiments females tended to lay more eggs in larger amounts of flour. However, in the largest amounts of flour there was a decrease in oviposition, which may be due to the physical structure of the artificial refugia. In the refugia with the most flour, the flour completely filled the gap between the glass slides. It has been suggested that physical characteristics of the container holding flour can influence the number of eggs laid (Campbell and Hagstrum, 2002).

After a female encounters a resource patch, the decision of how many eggs to lay is influenced by her physiological state and resource patch quality (Charnov and Skinner, 1985; Skinner, 1985; Mangel, 1989). In this study, we standardized physiological state as much as possible and varied patch quality. Adjusting oviposition in

Table 2. Size and sex ratio of *Tribolium castaneum* progeny developing in different amounts of flour.

Amount of flour (g)	Number of individuals	Elytra length (mm) (mean±sem)	Statistical differences	Sex ratio (proportion males)
0.005	6	2.48±0.10	c	0.67
0.01	12	2.52±0.05	c	0.43
0.02	16	2.70±0.03	ab	0.27
0.04	38	2.68±0.03	b	0.43
0.08	56	2.69±0.02	b	0.56
0.1	75	2.72±0.02	ab	0.49
0.2	60	2.74±0.02	ab	0.47
0.4	80	2.74±0.01	ab	0.46
0.8	95	2.78±0.01	a	0.58
1	91	2.79±0.01	a	0.46

Figure 4. Relationship between the number of eggs laid in a given amount of flour and the optimal predicted clutch size for that amount of flour (i.e., Lack clutch size).



response to patch quality is a widely observed phenomenon for insect parasitoids (Godfrey et al., 1991). A variety of seed parasites also evaluate seed size and adjust the number of eggs that they lay (Fox et al., 1996; Desouhant et al., 2000; Campbell, 2002). In these cases the larvae are restricted to the food resource selected by the mother and, therefore, offspring fitness is strongly influenced by the oviposition decision. Red flour beetles feed on damaged or processed seeds, but in many environments these resources occur in small patches. Larval movement among patches is likely to be limited and to incur significant risk of mortality, but we are not aware of any actual measurements of this behavior. The optimal adjustments in the average clutch size with changes in patch quality we observed suggests that *T. castaneum* has adaptations for exploiting spatially patchy resources, but the considerable individual variation indicates that other unaccounted for factors are also likely to be important in oviposition decisions. Some likely variables include female size, previous experience, egg limitation and perhaps multiple visits to a patch.

The number of eggs laid by female *T. castaneum* was consistent with the Lack clutch size prediction. Lack's hypothesis is that mothers should lay the number of eggs that maximizes her fitness from the whole clutch and that this optimal number of eggs is strongly influenced by the quality of the patch in which the clutch is laid (Godfray, 1994). Lack clutch sizes are only predicted to occur if maximizing lifetime fitness is equivalent to maximizing the fitness gains from a single clutch. In empirical tests of this model, most species tend to lay fewer eggs in a clutch than predicted by the Lack clutch size (Klomp 1970; Charnov and Skinner, 1984; Godfray et al., 1991). This discrepancy may result because costs of laying a clutch of a certain size on future reproduction are not taken into account. For insects, two major costs of reproduction are loss of time that could be used searching for new resources and loss of eggs that could be placed in more profitable patches. Both of these factors have been demonstrated to be important for parasitoid wasps (Godfray, 1994; Rosenheim, 1996). For long-lived beetles that lay

large numbers of eggs such as *T. castaneum* costs to future reproduction may be less and this could explain the closer relationship between observed and Lack clutch size observed in this study. Although there was a good correlation between *T. castaneum* oviposition and the Lack clutch size, the number of eggs laid per visit to a patch could not be determined and it is therefore possible that the total number of eggs laid in a patch may not represent a single clutch.

We do not know the specific behavioral mechanisms generating the differences in egg number among different amounts of flour. Visual, tactile and chemical cues may be involved in beetle evaluation of patch quality. Red flour beetles respond to some volatile components of grain (Barrer, 1983; Phillips et al., 1993). Ruano et al. (1970) found that clipping female antennae enhanced egg laying, suggesting that volatile or possibly contact cues are involved in regulating oviposition rate. Increased egg laying could result from females staying longer in larger patches than in smaller ones and therefore laying more eggs, from females laying more eggs per visit in larger patches than small patches, or from females laying the same number of eggs per visit but visiting larger patches more frequently. Based on the four patch experiment it does not appear that females are just spending more time in larger patches, except in the case where there was only one food patch. Further research on the specific behavioral mechanisms used to evaluate patches is needed.

Clearly, under more natural conditions a wider range of patch quality factors needs to be taken into account; including previous exploitation of the patch by con- and hetero-specifics. *Tribolium* spp. produce pheromones (Suzuki, 1980; Hussain, 1993) and have cuticular quinone and hydrocarbon secretions (Markarian et al., 1978; Howard, 1987) that, along with the presence of eggs, could indicate previous exploitation of a patch. It has been shown that previous conditioning of the flour by con- and hetero-specifics affects oviposition and dispersal (Ziegler, 1976), but it remains to be seen how it influences clutch size. In addition, the optimal clutch size for offspring can be different from that of the mother and this can lead to parent-offspring conflicts (Godfray and Parker, 1992). *Tribolium* larvae can be cannibalistic (Park et al., 1965; Stevens, 1989) and siblicide may be a mechanism by which offspring exert some control over clutch size. *Tribolium castaneum* has been used as a model organism for a wide range of genetic questions, but it also can be an ideal species for addressing behavioral ecology questions about patch exploitation that have both basic and applied application.

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References

Barrer PM. 1983. A field demonstration of odor-based, host-food

- finding behavior in several species of stored grain insects. *Journal of the Kansas Entomological Society* 63: 466-485
- Ben-Shlomo R, Motro U, Ritte U. 1991. The influence of the ability to disperse on generation length and population size in the flour beetle, *Tribolium castaneum*. *Ecological Entomology* 16: 279-282
- Birch LC, Park T, Frank MB. 1951. The effect of intraspecies and inter-species competition on the fecundity of two species of flour beetles. *Evolution* 5: 116-132.
- Campbell JF. 2002. Influence of seed size on exploitation by the rice weevil, *Sitophilus oryzae*. *Journal of Insect Behavior* 15: 429-445.
- Campbell JF, Hagstrum DW. 2002. Patch exploitation by *Tribolium castaneum*: movement patterns, distribution and oviposition. *Journal of Stored Product Research* 38: 55-68.
- Charnov EL, Skinner SW. 1985. Complementary approaches to the understanding of parasitoid oviposition decisions. *Environmental Entomology* 14: 383-391.
- Desouhant E, Debouzie D, Ploye H, Menu F. 2000. Clutch size manipulations in the chestnut weevil, *Curculio elephas*: fitness of oviposition strategies. *Oecologia* 122: 493-499.
- Fox CW, Martin JD, Thakar MS. 1996. Clutch size manipulations in two seed beetles: consequences for progeny fitness. *Oecologia* 108: 88-94.
- Godfray HCJ. 1994. *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton University Press, Princeton.
- Godfray HCJ, Parker GA. 1992. Sibling competition, parent offspring conflict and clutch size. *Animal Behavior* 43: 473-490.
- Godfray HCJ, Patridge L, Harvey PH. 1991. Clutch size. *Annual Review of Ecology and Systematics* 22: 409-429.
- Good NE. 1933. Biology of the flour beetles, *Tribolium confusum* Duv. and *T. ferrugineum* Fab. *Journal of Agricultural Research* 46: 327-334.
- Good NE. 1936. *The flour beetles of the genus Tribolium*. USDA Technical Bulletin 5: 27-28.
- Hagstrum DW. 1973. Infestation of flour by *Tribolium castaneum*: relationship between distribution of eggs and adults in a dispersing population. *Annals of the Entomological Society of America* 66: 587-591.
- Hagstrum DW, Gilbert, EE. 1976. Emigration rate and age structure dynamics of *Tribolium castaneum* populations during growth phase of a colonization episode. *Environmental Entomology* 5: 445-448.
- Hagstrum DW, Leach CE. 1972. Infestation of flour by *Tribolium castaneum*: rate of adult movement in relationship to sex, mated condition, and other factors. *Annals of the Entomological Society of America* 66: 384-387.
- Howard RW. 1987. Chemosystematic studies of the Tribolinni (Coleoptera: Tenebrionidae): Phylogenetic inferences from the defensive chemicals of eight *Tribolium* spp., *Palorus ratzeburgi* (Wissmann), and *Latheticus oryzae* Waterhouse. *Annals of the Entomological Society of America* 80: 398-405.
- Howe RW. 1962. The effects of temperature and humidity on the oviposition rate of *Tribolium castaneum* (Hbst.) (Coleoptera, Tenebrionidae). *Bulletin of Entomological Research* 53: 301-310.
- Hussain A. 1993. *Chemical ecology of Tribolium castaneum* Herbst (Coleoptera: Tenebrionidae): Factors affecting biology and application of pheromone. Ph.D. Thesis, Oregon State University
- Klomp H. 1970. The determination of clutch-size in birds: a review. *Ardea* 58:1-124.
- Lack D. 1947. The significance of clutch size. *Ibis* 89: 302-352.
- Lavie B, Ritte U. 1978. The relation between dispersal behavior and reproductive fitness in the flour beetle *Tribolium castaneum*. *Canadian Journal of Genetics and Cytology* 20: 589-595.
- Lomnicki A, Krawczyk J. 1980. Equal egg densities as a result of emigration in *Tribolium castaneum*. *Ecology* 61: 432-437
- Mangel M 1989. Evolution of host selection in parasitoids: does the state of the parasitoid matter? *American Naturalist* 133: 688-705.
- Markarian H., Florentine GJ, Pratt Jr., JJ. 1978. Quinone production of some species of *Tribolium*. *Journal of Insect Physiology* 14: 785-790.
- Naylor AF. 1961. Dispersal in the red flour beetle, *Tribolium castaneum* (Tenebrionidae). *Ecology* 42: 231-7.
- Ogden JC. 1970. Aspects of dispersal in *Tribolium* flour beetles. *Physiological Zoology* 43: 124-131.
- Park T, Frank MB. 1948. The fecundity and development of the flour beetles *Tribolium confusum* and *Tribolium castaneum* at three constant temperatures. *Ecology* 29: 368-374.
- Park T, Mertz DB, Grodzinski W, Prus T. 1965. Cannibalistic predation in populations of flour beetles. *Physiological Zoology* 38: 289-321.
- Phillips TW, Jiang XL, Burkholder WE, Phillips JK, Tran HQ. 1993. Behavioral responses to food volatiles by two species of stored-product Coleoptera, *Sitophilus oryzae* (Curculionidae) and *Tribolium castaneum* (Tenebrionidae). *Journal of Chemical Ecology* 19: 723-734.
- Rosenheim, JA. 1996. An evolutionary argument for egg limitation. *Evolution* 50: 2089-2094.
- Ruano RG, Barrera A, Orozco F. 1970. Influence of antennae clipping on egg laying rate of *Tribolium castaneum* females. *Tribolium Information Bulletin* 13: 77-81.
- Skinner SW 1985. Clutch size as an optimal foraging problem for insects. *Behavioral Ecology and Sociobiology* 17: 231-238.
- Sokoloff A. 1974. *The Biology of Tribolium: With Special Emphasis on Genetic Aspects*. Vol. 2. Clarendon Press, Oxford.
- Stanley MSM, Grundmann, AW. 1965. Observations on the morphology and sexual behavior of *Tribolium confusum* Duval. *Journal of the Kansas Entomological Society* 38: 10-18.
- Stevens L. 1989. The genetics and evolution of cannibalism in flour beetles (genus *Tribolium*). *Evolution* 43: 169-179.
- Surtees G. 1963. Laboratory studies on dispersal behavior of adult beetles in grain: III. *Tribolium castaneum* (Hbst) (Coleoptera, Tenebrionidae) and *Cryptolestes ferrugineus* (Steph) (Coleoptera, Cucujidae). *Bulletin of Entomological Research* 54: 297-306.
- Surtees G. 1964. Laboratory studies on dispersion behavior of adult

- beetles in grain. VI. Three-dimensional analysis of dispersion of five species in a uniform bulk. *Bulletin of Entomological Research* 55: 161-171.
- Suzuki T. 1980. 4, 8-Dimethyldecanal: The aggregation pheromone of the flour beetles, *Tribolium castaneum* and *T. confusum* (Coleoptera: Tenebrionidae). *Agricultural and Biological Chemistry*. 44: 2519-2520.
- Zar JH. 1999. *Statistical analysis*. 4th edition. Prentice Hall.
- Ziegler JR. 1976. Evolution of the migration response: emigration by *Tribolium* and the influence of age. *Evolution* 30: 579-592.
- Ziegler JR. 1977. Dispersal and reproduction in *Tribolium*: the influence of initial density. *Environmental Entomology* 7:149-156.