Influence of female age and grain availability on the ovipositional pattern of the wheat weevil *Sitophilus granarius* (Coleoptera: Curculionidae)

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**Abstract.** The ovipositional patterns of *Sitophilus granarius* females have been studied over time, and in response to different numbers of available wheat grains. The female fecundity and the degree of grain infestation show a maximum by 20th day of adult life, and a significant decrease after 30th day. Increasing grain availability leads to a rise of both female fecundity and grain infestation, until saturation is reached. The frequency distribution of the numbers of eggs per grain shows a contagious pattern due to a tendency of females to lay more than one egg within the same grain. This behaviour is independent of female age and grain availability, and consequently the possibility that it may be an adaptive reproductive strategy is discussed.

**INTRODUCTION**

Species of the genus *Sitophilus* are cosmopolitan pests of stored grain. Studies on the egg laying behaviour suggested that females tend to lay more than one egg on the same grain, leaving others uninfested (Fava & Springhetti, 1991). It is also known that the female inspects a grain before laying, indicating that the site of deposition may be selected on the basis of specific features. Irrespective of the number of eggs contained within a grain, a single larva normally reaches maturity, maybe because of limited food availability (Hullock, 1965; Golebiowska, 1969) and of larval cannibalism (Steffan, 1963).

The present study is upon the influence of female age and grain availability on the ovipositional behaviour of *S. granarius* females, the investigation of the pattern of egg distribution among grains and whether this pattern is modified by variations of the above parameters.

**MATERIAL AND METHODS**

All experiments were made using adults of *Sitophilus granarius* (L.) emerged not more than 24 h before testing. Insects were taken from a stock reared for some years on wheat (*Triticum aestivum*).

Effects of female age

Female egg deposition was scored at the end of five successive 10-days periods. Male and female pairs were distributed each in a plastic tube (14 mm wide, 100 mm high) containing 100 wheat grains, which was then closed with cotton flock. Tubes were kept in a constant temperature room at 27°C and 65% RH.

Oviposition was followed for up to 110 days, but to keep weevil manipulation to a minimum, two tests were run, using different insects. In the first test, weevils were handled frequently but for a short period. In this test, eggs were counted in each tube at the end of two 10-days periods (1st–10th day, 10th–20th day). After egg counts pairs were transferred to other tubes containing fresh wheat.
The second test was longer than the first, lasting 110 days, but weevil handling along time was scattered. Eggs were counted at the end of three 10-days periods (20th–30th day, 60th–70th day and 100th–110th day) separated by 30-days intervals. At the beginning of each counting period and of each interval, the pairs were transferred to tubes with fresh grains. Eggs laid during intervals were ignored.

In both experiments, infested grains and eggs were counted by random selection of 20 grains out of 100 from each tube. Grains were stained with acid fuchsin according to the Frankenfeld’s (1948) method. If a male died during experiment, it was replaced, while if a female died the tube was discarded. Thus the number of tubes was reduced to a total of 24 in the first test (female mortality was about 25%) and to 13 in the second one (female mortality was about 70%, mostly occurring in the last period). Statistics were performed on desktop computer using the SAS Software System, Release 6.04.

Effects of grain availability

Pairs of males and females were reared in vials of different kinds with different numbers of grains. The laid eggs were counted in a subsample of grains. In order to follow the activity of single pairs as long as possible, without emergence of new adults from the eggs laid by tested females, an experiment duration of 38 days was chosen. In all vials the grain mass had a similar thickness. Vials were kept in a constant temperature room at 27°C and 65% RH. The experimental design is detailed in Table 1. Egg counts and statistics were performed as described above.

| Table 1. Experimental design for testing the effects of grain availability on oviposition. |
|---------------------------------|-----------------|-----------------|-----------------|
| Group  | Type of container | Number of grains per container | Number of examined grains | Number of replicates |
| 1      | 100-mm long, 14-mm wide tubes | 30 | 20 | 14 |
| 2      | 100-mm long, 14-mm wide tubes | 60 | 20 | 14 |
| 3      | 73-mm long, 22-mm wide tubes rectangular box (5.5 x 4 x 1.8 cm) | 120 | 40 | 12 |
| 4      | rectangular box (5.5 x 4 x 1.8 cm) | 240 | 40 | 12 |
| 5      | rectangular box (5.5 x 4 x 1.8 cm) | 480 | 60 | 12 |

RESULTS

Effects of female age

In order to determine age-dependent variations in the oviposition of S. granarius females all data were combined, resulting in five sequential data sets. The first two sets (1st–10th day and 10th–20th day) concerned the group of females examined in the first test; the last three (20th–30th day, 60th–70th day and 100th–110th day) concerned different females examined in the second test.

The total of eggs laid and the number of infested grains varied as a function of female age (Table 2). According to the Duncan test, the average numbers of eggs laid by each female increased significantly from 10 to 20 days, decreased significantly from 20 to 70 days, and finally showed a non-significant decrease from 70 to 110 days (Table 2). The trend for the total number of grains infested was similar, although Duncan results were slightly different, showing no significant variation until 30 days, followed by a significant decrease (Table 2). For both eggs laid and grains infested data ranges were relatively high, indicating conspicuous variability among females. However, the trends of min. and max. values roughly followed the average values (Table 2).
For each of the five investigated ten-days periods, a frequency distribution of the numbers of eggs per grain was derived by combining data from all females. A goodness of fit test was made on the five observed distributions by comparing each of them with Monte Carlo samples extracted from Poisson distributions. A chi-squared test between the observed and the simulated Poisson frequency distributions found significant differences in the second period (p < 0.01). However, in all periods, except the fourth, variance was greater than mean, and in these cases a chi-squared test based on the variance/mean ratio gave significant differences from Poisson, suggesting a contagious pattern. The second period, showing maximum divergence from Poisson, corresponded to the maximum activity of egg laying (Table 2) and also showed the minimum correlation between number of eggs per grain and number of infested grains.

Effects of grain availability

The total number of eggs laid by each female increased from 30 to 120 available grains, showing minor fluctuations for higher numbers of available grains (Table 3). The corresponding numbers of infested grains showed a constant increase for increasing numbers of available grains (Table 3). As in the former experiment, data ranges were high, confirming a considerable ovipositional variation among females.

Data of both total eggs laid and numbers of infested grains suggested a saturation in the response of females to increasing grain availability (Table 3). For total eggs laid, the Duncan test formed two overlapping groups, consisting of the first two experimental units (30 and 60 available grains) and of the last four ones (60, 120, 240 and 480 available grains),
respectively (Table 3). For total numbers of grains infested, the test singled out the three first units and grouped the last two (Table 3).

The analysis of the frequency distribution pattern of the numbers of eggs per grain was made by the goodness-of-fit method, as described in the above section. The chi-squared test gave significant differences for all numbers of available grains (p < 0.05) except for 240 available grains, where the test results were equivocal. However, in all distributions there was variance > mean, while a chi-squared test based on the variance/mean ratio always found significant divergence from Poisson, suggesting also in this case a contagious pattern.

DISCUSSION

The experiment based on the age of females shows that in S. granarius the time oviposition pattern consists of an early maximum followed by a sharp decrease, presumably starting after the fifth week of female life. This pattern is different from previous reports concerning this species, where the time dependent curve was smoother due to a slower scaling down of the oviposition rate after the maximum (Steffan, 1963; Eastham & McCully, 1943; Richards, 1947). Conversely, the present data are similar to reports concerning S. oryzae females (Steffan, 1963; Segrove, 1951). Such a mismatch could be partially explained by a difference in the experimental temperature, which was 25°C in the literature-reported experiments on S. granarius and 27°C in our case. In weevils, increasing temperatures make female life shorter and oviposition rate higher (Eastham & McCully, 1943), and it is therefore conceivable that the shape of oviposition-vs-time curves changes from dome-like to cusped as the temperature increases. Another possible explanation comes from the occurrence of variable offspring production rates in different strains of S. granarius (Longstaff, 1981a), suggesting that such intraspecific variability could also involve time oviposition patterns.

In the test of different grain availability, although the two lowest numbers of available grains, i.e. 30 and 60, could limit maximal responses of females, data of grain infestation clearly show that for higher numbers of available grains female fecundity increases. Also, in this experiment grain availability roughly simulates different population densities, and our oviposition curve fits the results of an analysis on population density effects in S. oryzae (Longstaff, 1981b). The female age experiment showed that most ovipositional effort is concentrated within the first 30–40 days of life, and therefore the experiment on grain availability, which lasted 38 days, roughly yielded total female oviposition potentialities. While grain availability was increased beyond 120 grains, the female total effort did not exceed the values of about 200 laid eggs and 130 infested grains, which can therefore be assumed as a rough estimate of the average female infestation potentiality.

The goodness-of-fit and the variance/mean tests both confirm the tendency of S. granarius females to lay more than one egg within the same grain. Moreover, our data indicate that, at least to some extent, such an ovipositional behaviour is independent from environmental conditions.

A contagious distribution pattern implies that the laying of one egg within a grain increases the probability that another egg is laid there. In S. oryzae, Nardon et al. (1981) tried to explain this behaviour assuming limited territory exploration by females, which would leave distant grains uninfested, hence simulating contagious oviposition. Our
analysis does not confirm this view, as the pattern seems independent of grain availability. Springhetti and Fava (unpublished) also question the hypothesis that in small vials repel- lent substances from infested grains could saturate the space and lose their action in selectively preventing oviposition.

Assuming that the tendency to clump eggs within grains does not depend on experimental conditions, some adaptive meaning could be postulated. At first sight such a trait would seem disadvantageous, since only one larva per grain normally develops, and therefore a uniform or even a random egg distribution could yield higher offspring survival. However, cannibalism occurring within grains could enhance the survival of cannibalistic larvae, hence compensating for reproductive costs and ultimately increasing fitness. This hypothesis is supported by the fact that in flour beetles there is a genetically-controlled larval cannibalism (Stevens & Mertz, 1985; Stevens, 1989) which is known to enhance both immature survival (Mertz & Robertson, 1970) and later adult fecundity (Ho & Dawson, 1966). If confirmation of the above hypothesis were achieved through directed experiments on Sitophilus, oviposition patterns could be interpreted within an evolutionary framework.

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REFERENCES


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