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Diffusion of Rusty Grain Beetles in Stored Grain Bulks

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Abstract
Insect movement inside a stored grain bulk increases the chance for the pests to find biologically suitable locations for their development and multiplication. The movement of rusty grain beetle adults in 3, 12, 24, and 72 h was determined in a $0.1\times1\times1$ m wooden box filled with $14.5\pm0.2\%$ moisture content (wet basis) wheat at $30\pm0.5°C$. The average diffusivity of the adults at the tested condition was $(7.3\pm0.1)\times10^{-4}$ m^2/h. There was no significant difference between measured and predicted insect numbers using a diffusion model. Statistical tests were conducted and it was verified that the distribution and dispersal of the adults followed a diffusion pattern.

Key words: Stored grain, *Cryptolestes ferrugineus,* Movement, Diffusion.

Introduction

Rusty Grain Beetle, *Cryptolestes ferrugineus* (Stephens) (Coleoptera: Laemophloeidae), is a prevalent pest of stored grain throughout the world (Howe and Lefkovitch 1957). Seasonal and daily weather changes cause temperature gradients in bulk grain in granaries, and the temperature fluctuation causes moisture gradients and migration (Jayas 1995). The adults of the beetle move inside a grain bulk in response to the variations of temperature (Flinn and Hagstrum1998, Jian et al. 2002, 2003, 2004a, 2004b), moisture (Loschiavo 1983, Jian et al. 2005), carbon dioxide (White et al. 1993), dockage (Jian et al. 2005), light (Loschiavo 1974), and insect density (Jian et al. 2004a). There are no reports about how one beetle moves (such as random or bias movement) because there was no available equipment until now to trace an individual beetle inside a grain bulk. Therefore, their distribution and response to these factors are determined by the measurement of their net displacement (Jian et al. 2002, 2003, 2004a, 2004b, 2005) or insect number (density) at different distances (insect density-distance measurement) (Loschiavo 1983, White et al. 1993) from their introduction position at different time intervals by using mass release and recovery techniques. Measurement of the net displacement is a better measure of what the "average individual" does, but can be misleading due to the very leptokurtic nature of most dispersal distance (such as the dispersal at a temperature gradient), and does not provide the information about the variance in dispersal distances that is of crucial importance in predicting population spread and distribution. Density-distance measurement solely derived from the distribution lack an explicit temporal component (Turchin 1998).

To predict insect movement and distribution and to simplify the developed models, behavioral minimalism is used (Lima and Zollner 1996) because it is impossible to know how insect truly move and what is the driving force to motivate insect movement. Even if possible, the dispersal model will not include all of the motivation parameters, since such a model would have an enormous number of parameters and would requires a very accurate representation of all environmental "micro-cues" (Turchin 1998). The behavioral minimalism assumes that: 1) the behavior of an individual is erratic, or irregular, and each individual could be a perfect automaton, rigidly reacting to environmental cues; and 2) the redistribution process at the population level has many regular features. Because diffusion is closely connected with this transfer phenomenon, diffusion has been used to model insect movement (Banks et al. 1985).

The diffusion rate (diffusivity), D, is a parameter in a diffusion model. D has some theoretical support since it: 1) combines both the mean and the variance in the dispersal distance of insect distribution; and 2) explicitly incorporates the time element because it is the temporal rate of population spread and distribution. However, D should not be used to infer the rate of population redistribution and spread unless it is first shown that the mode of dispersal conforms, at least approximately, to the assumption of the simple diffusion model (Kareiva 1982).

The aim of this study was to verify if the movement of the rusty grain beetle can be described by diffusion using a comprehensive test approach approved by Kareiva (1982).

Material and methods

Wheat Hard red spring wheat (grade No.1, cv. 'AC Barrie' certified) was used in all of the experiments. The wheat was moistened in a rotating drum to obtain the desired moisture

content (14.5±0.2%). The wheat moisture content was determined using a standard oven-drying method by drying triplicate 10-g samples at 130°C for 19 h (ASAE 2002).

Insects *Cryptolestes ferrugineus* were reared at 30±1°C and 75±5% relative humidity on cracked wheat plus wheat germ (95:5, wt:wt), and were held in the dark during rearing and during experiments. The cultures of *C. ferrugineus* had been reared in the laboratory for over 3 years. The adults of mixed sex were 1 day to 2 months old at the start of each experiment. Before introducing the beetles into the grain chamber, 250 adults were selected from the jar and held in a 20-ml glass vial (covered by a lid made of 0.5 mm opening screen) with about 10 g wheat. The glass vial was kept in a 2.7×2.7×2.2 m environmental chamber (Conviron CMP3244, Controlled Environments Ltd., Winnipeg, MB, Canada) for 24 h to acclimate the adults at 75% RH and 30±0.5°C.

Grain chamber The grain chamber (Fig. 1) is a 1×1×0.1 m (inside dimension) wooden box (referred to as 2-dimension or 2-D box) with 1×1 m wooden cover. The sides of the 2-D box were made by 4 cm thickness wooden boards. The base and cover were made by 1 cm thickness wooden boards. There is a 5 cm diameter hole at the center of the cover. Insects were introduced through this hole. During experiment, the hole was plugged by a rubber stopper. The inside surfaces of the cover and base were covered by 2 mm thick expansion Styrofoam.
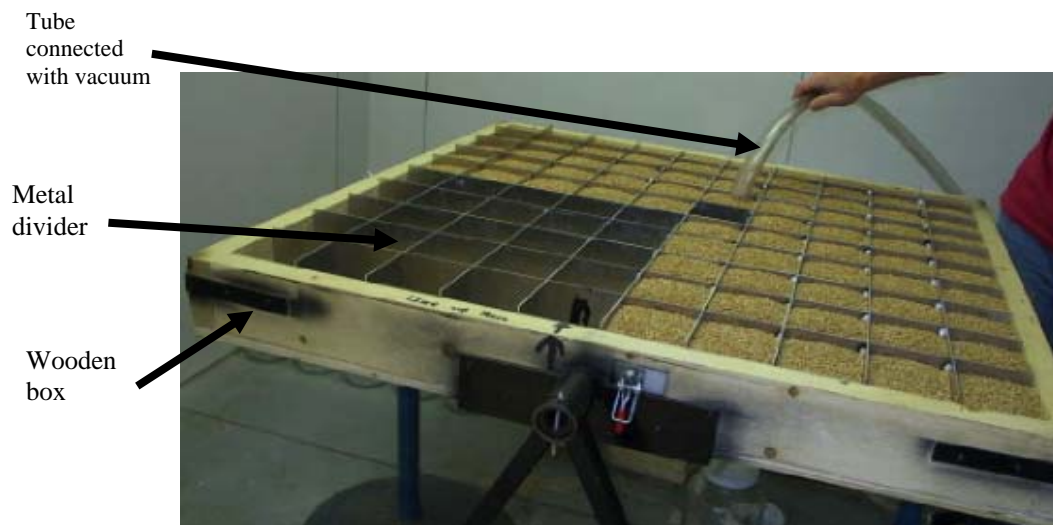

Fig. 1 The grain chamber used to test beetle movement.

Testing procedure The wooden box filled with wheat was kept in the environmental chamber at a constant temperature of 30±0.5˚C and 75±5% RH for at least 4 days before the beetles were introduced. A plastic tube (4.8 cm external diameter with 0.2 cm thickness) with a wooden rod inside the tube was pushed into the center of the 2-D grain chamber through the introduction hole at the center of the cover. After the wooden rod was pulled out, the acclimated 250 adults were introduced into the tube, and then the tube was pulled out. Three, twelve, twenty-four or seventy-two hours after the introduction, the wood cover was removed and a metal divider was inserted into the box (Fig.1). This method divided the box into 100 equal sections and each section was 0.1×0.1×0.1 m. The wheat in each section was sucked into a 5-L bottle using gentle vacuum. The

adults in each section were separated from the wheat and counted using the method descried by Loschiavo (1974). For all tests, the recovery rate of the adults was 96.3±0.9% (n = 12) because some adults might remain in the sieved wheat. During the data analysis, the number of the recovered adults from each replication was adjusted to 250 (number of adults in the section = number of the recovered adults in the section × 250/number of the recovered adults in the box) for comparison.

Insect number calculation   Insect number in each section at a time period in the 2-D grain chamber was calculated using the following equation (Carslaw and Jaeger 1959):

$$u(x, y, t) = \frac{N_0}{AB}\{1 + 2\sum_{n=1}^{\infty} e^{[-D(\frac{n\pi}{A})^2 t]} \cos[\frac{n\pi}{A}(x+\frac{A}{2})]\cos(\frac{n\pi}{2})\} \times$$

$$\{1 + 2\sum_{n=1}^{\infty} e^{[-D(\frac{n\pi}{B})^2 t]} \cos[\frac{n\pi}{B}(x+\frac{B}{2})]\cos(\frac{n\pi}{2})\}$$

(1)

Where, x and y are the coordinate at the center of the section;
$u(x,y,t)$ is the insect number in the section (adults/m^3 at time t);
N_0 is the initial insect number (250 at the center of the 2-D chamber);
A and B are the length of the 2-D chamber (A=B=1 m);
n is set to 1 to 30 during the calculation;
D is the diffusion rate (diffusivity, m^2/h).

The algorithm to find the D at a movement period t was:
1) Initial guess of the diffusivity D (started from 0 to 0.005 m^2/h with a 0.00005 increment).
2) Calculated the insect number in each section in the movement period using equation 1.
3) Calculated the sum of the squared difference between the calculated and determined insect number in each section in the movement period.
4) Found the least squared difference (R^2) and assigned the guessed D as the diffusion coefficient at the testing temperature in the movement period (least square fit).

Data analysis To verify if the beetle movement is a simple diffusion, the following procedure was conducted:
1) The average D was calculated by pooling the D values at different movement periods.
2) The insect number in each section at a time period was predicted by using the calculated average D and equation 1.
3) The predicted and measured insect numbers in each section at a movement period were compared using the nonparametric Kolmogorov-Smirnov and Wilcoxon testes. Kolmogorov-Smirnov determines if there is significant difference of beetle distribution in the grain chamber at a movement period. Wilcoxon testes difference in locations at each section of the grain chamber.

Result and discussion

The average diffusivity at different movement periods was $(7.3\pm0.1) \times 10^{-4}$ m^2/h with a least square difference of 362.7±25.2 (n^2, n=insect number) (Table 1). There was no significant difference between the predicted and measured insect numbers in each movement period except of at 72 h with the Kolmogorov-Smirnov test (Table 2, Fig. 2). This statistical test procedure constitutes a stronger test of the simple diffusion than simply testing for normality. This test will reject the null hypothesis (simple diffusion) not only when the distribution of insects are normal,

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but also when the diffusion rate changes with time (Turchin 1998). Therefore, the difference between the predicted and measured insect number at 72 h might be caused by the small diffusivity at 72 h (Table 1). There was no significant difference between predicted and measured insect number using the calculated diffusivity at 72 h (Fig. 2 and 3, Table 2). These results verified that: 1) the movement of the beetles inside the homogeneous grain chamber follows a diffusion pattern; and 2) higher insect density in the introduction sections at the beginning of the introduction might increase insect dispersal.

Table 1. Calculated diffusivity (D) at different movement periods

Movement period (h)	D (mean±SE)×10^{-4}m^2/h	R^2 (mean[a]±SE)
3	8.0±1.9	338.4±25.6
12	9.6±2.5	331.2±13.3
24	7.8±2.4	351.2±96.6
72	3.5±0.5	429.9±36.2
Average	7.3±0.1	362.7±25.8

[a] The unit of the mean is the square of the insect number.

Table 2. Result of the statistical tests between measured and predicted insect numbers in the 2-D chamber at different movement periods

Movement period (h)	Wilcoxon		Kolmogorov-Smirnov	
	Z	P>Z	KSa	P>KSa
3 [a]	-0.3035	0.7615	0.7018	0.7081
12 [a]	0.9658	0.3344	1.0402	0.2294
24 [a]	-0.0498	0.9603	0.5320	0.9397
72 [a]	-1.1314	0.2582	1.6498	0.0086**
72 [b]	-1.5840	0.1132	1.1058	1.1773

[a] Compared between insect numbers measured and predicted using the average diffusivity.
[b] Compared between insect numbers measured and predicted using the calculated diffusivity at 72 h movement.
** Means there is a significant difference between the predicted and measured insect distribution at $P < 0.01$, using the Kolmogorov-Smirnov test.

Diffusion models and random walks are closely connected. Diffusion models provide continuum approximations of insect dispersal. However, the behavior minimalism approach to distribution and dispersal does not have to assume that the movement of each individual is completely random (Okubo 1986). This approach is successfully used in the thermodynamics and flow mechanics. The diffusion model has also been successfully used in the simulation of animal movement (Skalski and Gilliam 2000). Therefore, diffusion theory might be used to model the movement and dispersal of the rusty grain beetle even though it was not known if the movement of the beetles are truly random or not.
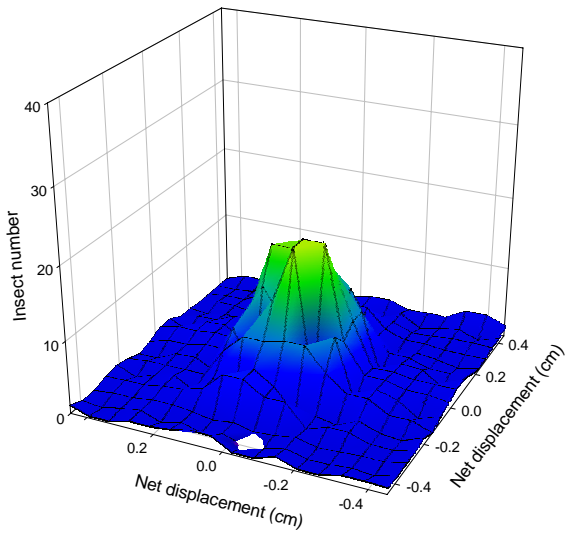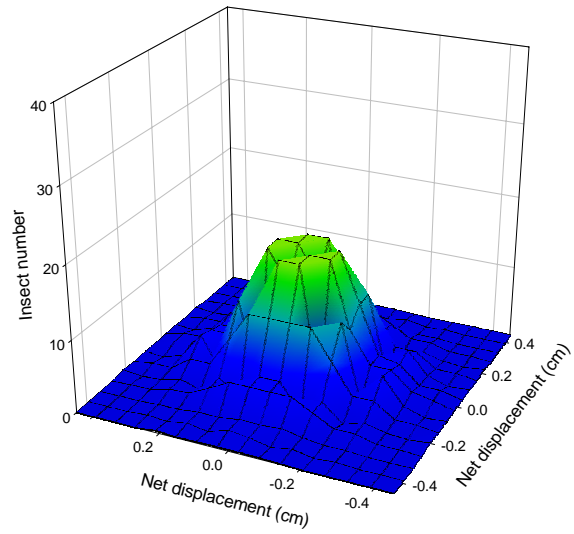
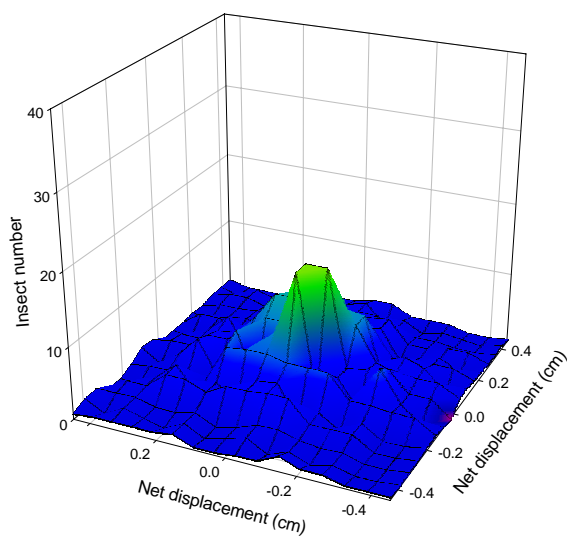## Acknowledgements
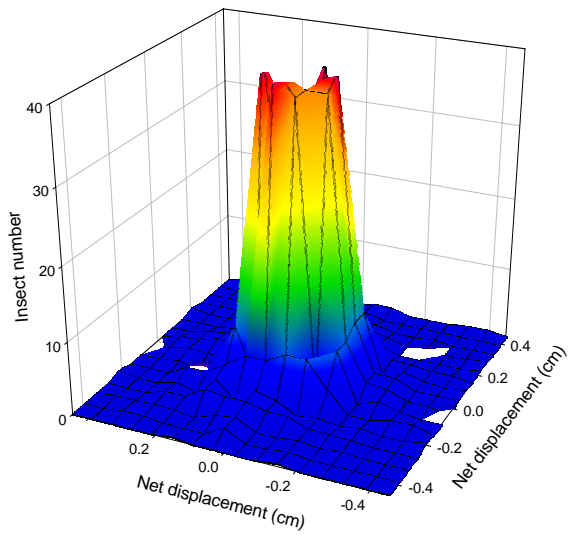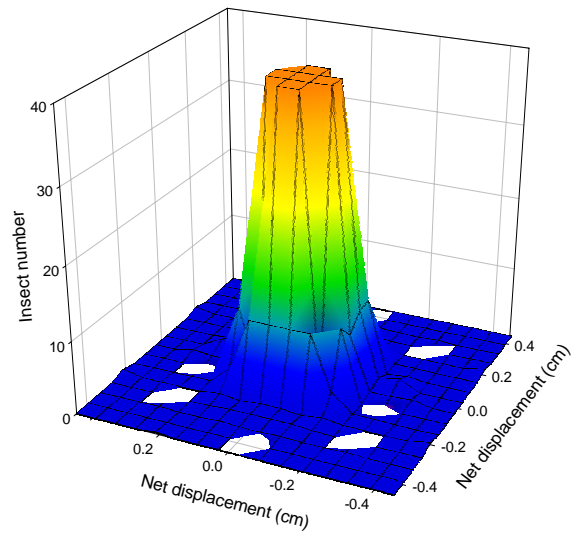
Measured at 3 h

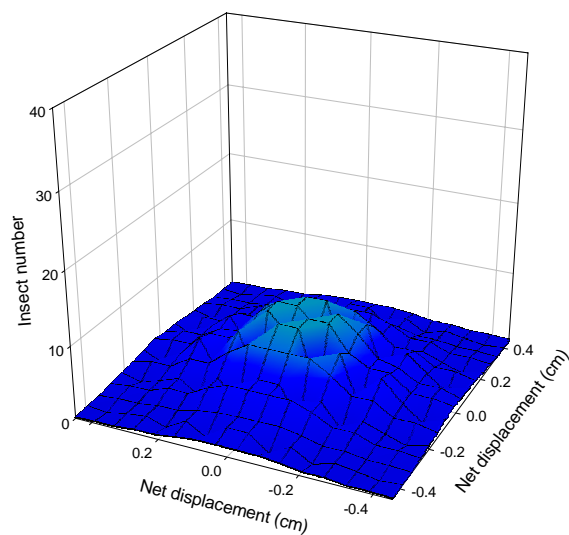Predicted at 3 h

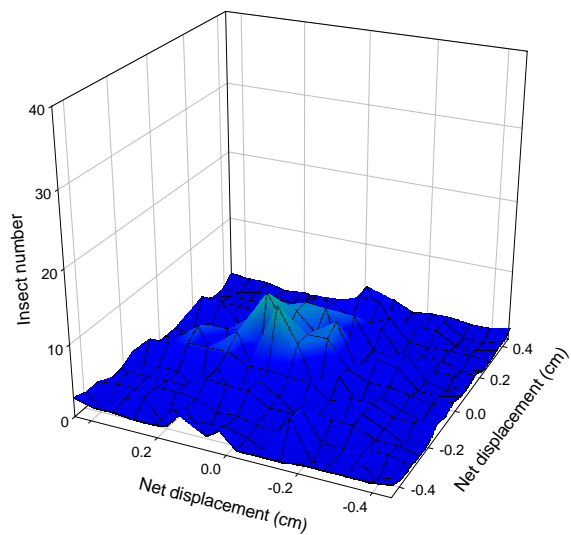Measured at 12 h

Predicted at 12 h

Fig. 2 Measured and predicted insect numbers at different insect movement periods (250 adults was initially introduced in the centre of the grain chamber in each replication, n =3)
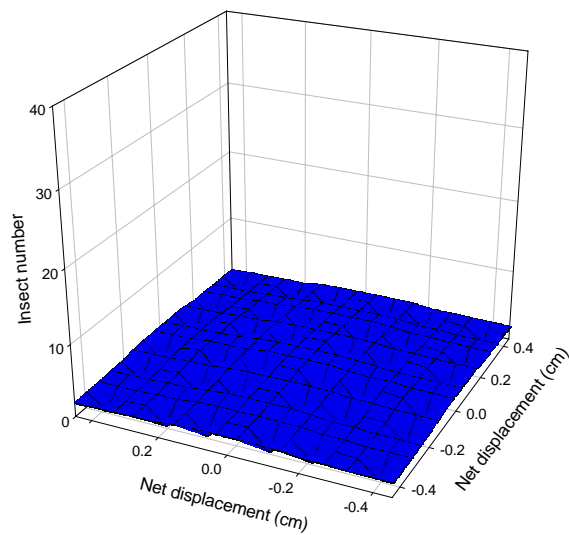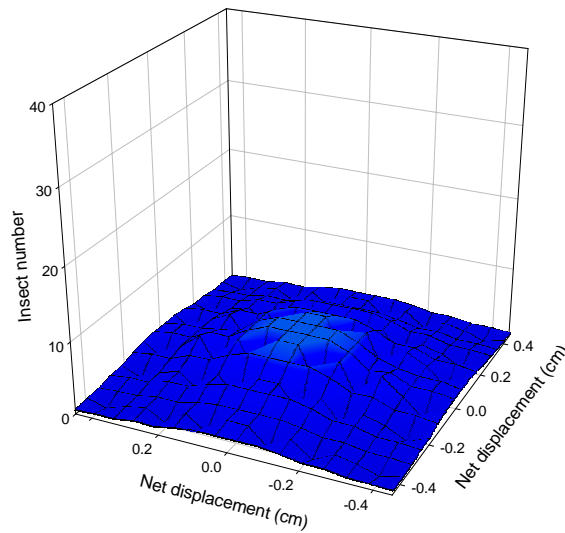
Measured at 24 h

Predicted at 24 h

Measured at 72 h

Predicted at 72 h

Fig. 2 continued

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Predicted at 72 h

Fig. 3 Predicted insect number in the grain chamber using the calculated diffusivity at 72 h

movement period.

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