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Research

Movement and Distribution of *Cryptolestes ferrugineus* (Coleoptera: Laemophloeidae) Adults Under Different Temperature Differences in Different Lengths of Horizontal Grain Columns

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Abstract

Understanding insect movement and distribution is critical for developing an effective insect pest management protocol. Movement and distribution of adult *Cryptolestes ferrugineus* (Stephens) in response to nominal temperature differences of 5, 10, 15, and 20°C in 1- and 2-m horizontal columns filled with 12.5% moisture content wheat were studied in 24, 48, and 72 h of movement times. In the wheat columns without temperature differences, adults had a diffusion distribution pattern caused by their random movement. Adults showed bias movement to the warmer grain in wheat columns with temperature differences and preferred the warmer grain regardless of the magnitude of temperature differences in less than 24 h. Their distribution did not have significant differences among different movement times in 1- or 2-m columns. About 40% of adults moved to the warmer wheat located at 0.4 to 0.5 m in the 1 m column but did not move to the warmer wheat located at 0.9 to 1 m in the 2-m column. Therefore, length of grain column influenced detection of warmer grain by insects. Adults under different temperatures had a similar response as that under linear temperature gradients.

Key words: adult movement, temperature difference, length of grain column, bias movement, wheat

Insect infestation of stored grains is one of the major factors for the depletion of stored grain quality and quantity. The spoilage of the harvested crops accounts for about 30% of the loss during the handling and storage which is mainly due to biological factors such as insects, pests, and molds (Srivastava and Mishra 2021). Wheat is considered as one of the major staple food crops and is widely consumed globally. Global production of wheat for the fiscal year 2020–2021 was estimated to be around 772.6 million metric tons (Statista 2021). The total loss of wheat was estimated to be as high as 4.3% during handling from harvesting to retailing (Kumar and Kalita 2017).

Among the existing stored product insects, the rusty grain beetle [*Cryptolestus ferrugineus* (Stephens) (Coleoptera: Laemophloeidae)] and red flour beetle [*Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae)] are mainly responsible for economic loss of stored wheat, especially in United States and Canada (Anukiruthika et al. 2021). Understanding the movement and distribution of insects helps us to develop a sampling plan, evaluate insect infestation rate, and conduct efficient storage management practices such as applying pesticides, leveraging monitoring tools, and properly specifying mathematical elements (Jayas 1995, Anukiruthika et al. 2021). However, determination of insect behavioral response is quite complicated with varying storage conditions and changing biotic and abiotic factors. The movement and distribution of stored product insects are affected by various biotic and abiotic factors and interactions among the factors (Mason 2019). Factors mainly affecting insect movement and distribution are temperature, moisture, and carbon dioxide and their gradients, grain type, dockage, broken kernels, grain mass, insect density, age, life stage and sex, chemical compounds, fumigants, and species–species interactions (Anukiruthika et al. 2021).

Over the past decades, several studies were attempted to understand this complex interrelation of stored grains and stored product insects (Willis and Roth 1954; Surtees 1963; Yinon and Shulov 1969; Adler 1992; Cordeiro et al. 2016, 2019). The complexity associated with tracing the movement and distribution of insects was reduced by developing a simple experimental setup or prototype models of actual grain storage structures. As an initial attempt, the distribution pattern of adult *C. ferrugineus* in stored wheat was studied under varied temperature gradients (Flinn and Hagstrum 1998).

Results showed the preference of insects towards warmer regions of arena. Similar studies were reported on determining the preference of insects under major individual gradients like temperature (Flinn et al. 1992, Kim et al. 2015, Henry and Wlodkowic 2020), moisture (Parde et al. 1998, Collins and Conyers 2009), and gas concentration (Navarro et al. 1981, White et al. 1993, Parde et al. 2004). Directional movement of insects was assessed in one-dimensional (1D) and two-dimensional (2D) grain mass. Insects have a bias diffusion under different temperature gradients, moisture differences, dockage levels, grain types and grain masses, time periods in relation with insect density, age, and temperature acclimation as summarized in a recent review on insect movement by Anukiruthika et al. (2021). Some of these studies focused on determination of the 1D vertical and horizontal movements of insects under a controlled linear temperature gradients (Jian et al. 2004a, 2005b). However, temperature sensing ability of beetles and their response of randomness or bias movements in relation to how much distance they could travel in grain mass are unclear.

Also, the temperature difference in stored grain bins rarely has linear distribution. Hence, study of insect movement under nonlinear temperature differences is important for practical applications and for developing mathematical models of insect distribution. In addition, no work is available on sensing ability of insects under different temperature differences in grain mass. To fill this knowledge gap, the objective of this study was to assess temperature response of adults of *C. ferrugineus* under nonlinear temperature differences in 1- and 2-m columns of wheat with 12.5% moisture content.

Materials and Methods

Wheat Temperature

Canada hard red spring wheat (certified no. 1, cultivar: AAC Brandon) was used in this study. The moisture content of the wheat was determined by following ASABE standards (ASABE 2020). The initial moisture content (m.c., wet basis) was 11% and was conditioned to 12.5 ± 0.04% by adding desired amount of distilled water (Jian et al. 2002). For example, 15 kg of 11% moisture wheat was mixed with 260-ml water in a mixer for 30 min. The conditioned wheat was kept in double layer plastic bags for moisture equilibration at 10°C for at least 2 wk until to be used for experiments. The plastic bags with the conditioned wheat were placed inside an environmental chamber maintained at 20°C and 75% r.h. for 5 d for temperature equilibration. Once the wheat reached 20°C, the grain column was filled by this tempered wheat. After the wheat was loaded into the grain column, the m.c. of the wheat was measured, and this moisture content was reported as the grain m.c. in this study.

Insects and Acclimation

Adults of *C. ferrugineus* of mixed sex with 2 d to 2–mo old were used in this study. The insects were reared at 30 ± 1°C and 75 ± 5% r.h. on a feed mixture of 90% whole wheat (14% m.c.), 5% cracked wheat, and 5% wheat germ (mass basis). One hundred adults from the culture were aspirated into a separate glass vial (0.8 cm diameter and 2.5 cm in length) filled with about 10 g of the conditioned wheat. The vial was loosely sealed with a perforated lid. To acclimate the adults, vials with the selected adults were kept inside the environmental chamber (Conviron CMP3244, Controlled Environments Ltd., Winnipeg, MB, Canada) set at 20°C and 75% r.h. for about 24 h.

Horizontal Grain Column

Adult movement was studied in six horizontal grain columns of 1 or 2 m length. The studies in 2-m columns were conducted after the 1-m column studies were completed. The dimension of the grain columns was 0.1 × 0.1 × 1 or 0.1 × 0.1 × 2 m (Fig. 1). For the ease of readability, the horizontal grain columns are referred to as grain columns from this point onwards. The material, structure, and insulation of the columns were similar as the columns used by Jian et al. (2002) without the use of a copper rod assembly to create temperature gradients along the wheat columns. In this study, grain columns were made using 19-mm thick plywood. One-sided sticky foam tapes were used at the connection of the four sides of the grain columns (1 and 2 m) and a top wooden lid to prevent the adults from escaping. One end of each grain column was cooled through conductive end-wall exposed to the surrounding temperature of the environmental chamber. Another end of each column was made of copper plate which was attached to copper coils. The copper coils were connected to a water bath (Thermo Scientific Precision Circulating water bath TSCIR 35, Fisher Scientific Company,

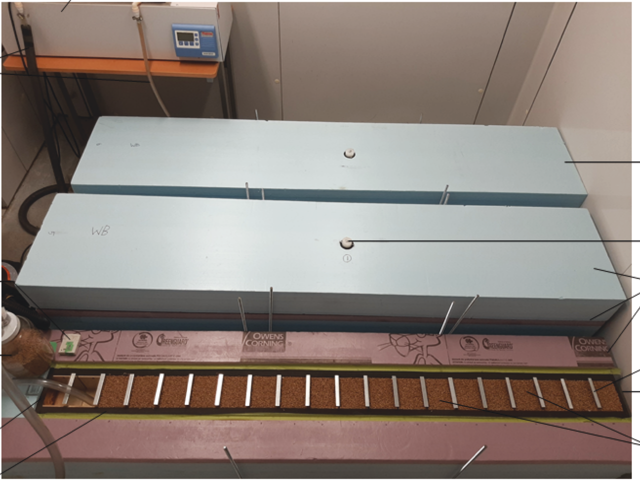

Fig. 1. Photograph of the 2-m grain column (0.1 × 0.1 × 2 m) experimental setup used in this study.

Ontario, Canada) through plastic water tubes. An external circulating pump was used to circulate the water through water tubes, water bath, and copper coils. The temperature of wheat in contact with the copper plate was controlled by the water bath temperature. The water bath temperature was set at cool end temperature (20°C) + nominal temperature difference + 5°C. For instance, to create 5°C temperature difference (referred to as 5°C-D), the water bath temperature was set at 30°C.

The conductive end wall was made of iron mesh plate of 10 mm thickness with 420 µm openings. A cloth mesh screen with opening < 1600 µm was attached to the conductive end wall at the inner side of the column to prevent the escape of insects. A plastic tube of 40 mm inner diameter, 4 mm wall thickness, and 160 mm length was fixed at the middle of the wooden lid of a grain column. The acclimated adults were introduced through this upright tube. A wooden plug with dimensions that tightly fitted the tube was used to close the tube during the test period. At the end of insect movement period, the top wooden lid of the grain column was removed, and the column was partitioned with thin metal (steel) slats (101 mm ×110 mm) inserted into the grain column to form 10 grain sections (Jian et al. 2002). Each section was 0.1 × 0.1 × 0.1 m. For the 2 m wheat column, 20 grain sections were generated.

Testing Procedure

Three grain columns (1 or 2 m), pump, and water bath were located inside the environmental chamber set at 20°C and 75% r.h. Before filling the three grain columns, 10 or 12 HOBO data loggers (Onset Computer Corporation, Bourne, MA) were evenly placed in each 1- or 2-m grain column, respectively. The grain temperatures recorded by each HOBO were retrieved using HOBOware software (ver. 3.7.22). The empty column was then filled with the prepared grain by compressing and packing the grains in a compact manner to make sure there was no gap between the lid and compacted wheat. Filling of wheat in the columns was done in the environmental chamber, so the wheat was kept at 20°C. To create a desired temperature difference inside the wheat column, water bath was set at the desired temperature according to the experiment design. Once the desired temperature was attained at copper coil end of the grain column (about 30 min after water bath was started), insects were introduced through the tube located at the middle of each column by pulling out the wooden plug before adult introduction. After the introduction, the wooden plug was relocated at its previous position. At the end of the insect movement, the grain column was partitioned into 10 or 20 grain sections for 1- or 2-m columns, respectively; and the grain from each section was carefully removed using a vacuum. The adults were separated from the collected grains by sieving the samples with a sieve (no. 20 with 850 µm opening). The beetles were counted by placing them in a porcelain tray and aspirated into a glass vial. The recovery ratio of the insects was determined from each section along the 1- and 2-m grain columns. All the experiments were done in triplicate. After removal of the wheat at the end of the experiment, the grain columns were thoroughly cleaned using a vacuum, and the columns were exposed to 20°C air stream for at least 12 h before the start of the next experiment.

Data Analysis

Experimental Design and Data Normalization

Adults were introduced at the middle of each grain column and this location was coded as '0 m distance from the introduction location'. The middle location of each section to this 0 m distance was used to code the insect movement distance to this location, and the distance at the water bath side (warmer) was assigned as positive (referred to as sections with Positive Distance), while opposite side was negative (referred to as sections with Negative Distance). This experimental code was also used to describe the temperature distribution in the columns because the HOBO sensors were also located at the middle of each section (Figs. 2–4; Table 1).

The response of adults to nonlinear nominal temperature differences of 0, 5, 10, 15, and 20°C in 1- and 2-m columns were studied in the movement periods of 24, 48, and 72 h (Table 1). Measured temperatures along the columns for all experiments are shown in Fig. 2. The water bath temperature was different from the temperature of wheat adjacent to the water bath. The temperatures in columns were not linear and were similar to temperatures as observed in wheat bins. To consistently present these data, the temperature difference was referred to as nominal temperature difference (referred to as °C-D in the experimental code). To understand the temperatures differences along the columns, multiple temperature differences were calculated (Table 1). All the data were presented as Mean ± SE (n = 3).

The overall recovery ratio of introduced adults in this study was 96.9 ± 0.2% (n = 90). To conduct statistical analysis at the same level, the recovered adults from each section were normalized,

$$\textit{Normalized insect count in the section} = \frac{N_S}{N_R} N_I \qquad (1)$$

where N_S is the recovered adults from the section, N_R is the recovered adults from the entire grain column, and N_I is the introduced adults in the grain column.

These normalized values were used to determine adults' movement. The movement and distribution of *C. ferrugineus* adults at different temperature differences and different time periods were compared by performing two-sample location tests and empirical distribution function (EDF) statistics. The Wilcoxon option and Median option were used for determining the difference in location and median difference in locations, respectively. The Kolmogorov–Smirnov (KS) option was used to test the difference in the distribution of beetles in grain column among the different temperature differences (Jian et al. 2004a). All these statistical analyses were performed using SAS software (SAS OnDemand for Academics) at α = 0.05 level SAS Institute (2004).

Results

Temperature Distribution in Grain Columns

The wheat temperature in each section under the control condition (water bath was not started) was 20.1 ± 0.0°C for both 1- and 2-m grain columns. After the water bath was started and the desired temperatures were set (Table 1), wheat temperature in sections close to water bath gradually increased nonlinearly (Fig. 2). The temperature differences between different points along 1- and 2-m columns under different experimental conditions are presented in Table 1. The temperature increases were mainly in the end sections with Positive Distance except for the 20°C-D in 1-m column at the end of the insect movement period (72 h) (Fig. 2). Therefore, if more than 50% of introduced adults moved to this end, this indicated the adults could detect the warmer grain and temperature difference. For example, at 5°C-D in 1 m column, the wheat temperature at 0.45, 0.05, and −0.45 m were 23.2 ± 0.4, 19.2 ± 0.7, and 19.9 ± 0.3°C, respectively at 0 h (adults introduced at this moment). After 24 h of adult movement, the temperature at these locations increased to 27.1 ± 0.1, 20.1 ± 0.1, and 20.2 ± 0.1°C,

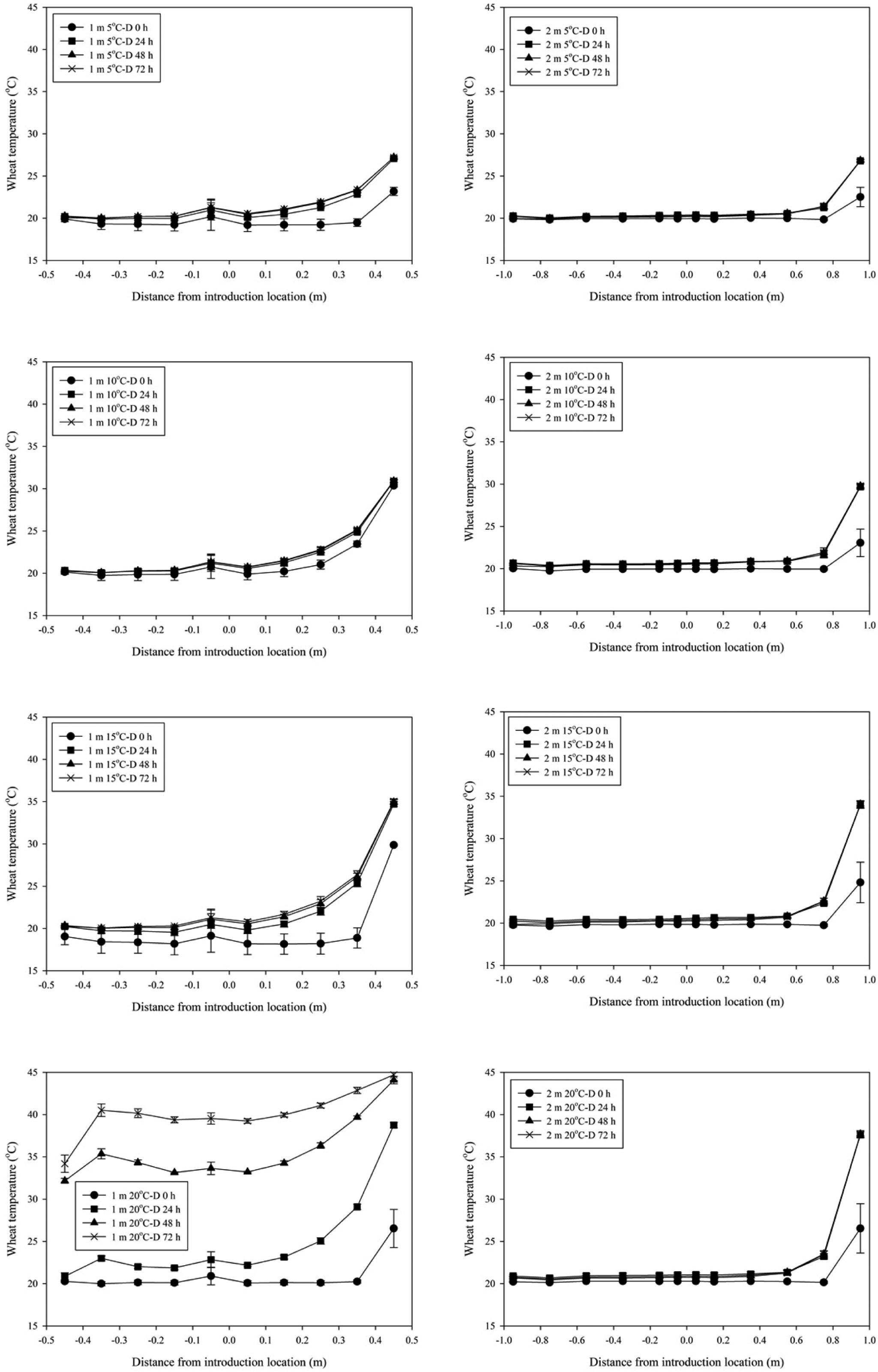

Fig. 2. Temperature distribution in grain columns under different experimental conditions. In the legend, 1 or 2 m is the grain column length. The number after 1 or 2 m is the nominal temperature difference between the two ends of the column, and number before h is the time after adult introduction (all data are presented as Mean ± SE, *n* = 3).

respectively. After 48 h, the temperature at each location became relatively stable and were 27.2 ± 0.1, 20.5 ± 0.1, and 20.3 ± 0.0°C, respectively.

Temperature change in columns was influenced by water bath temperature and the temperature difference between the water bath and the other end of the column (the cold end). The

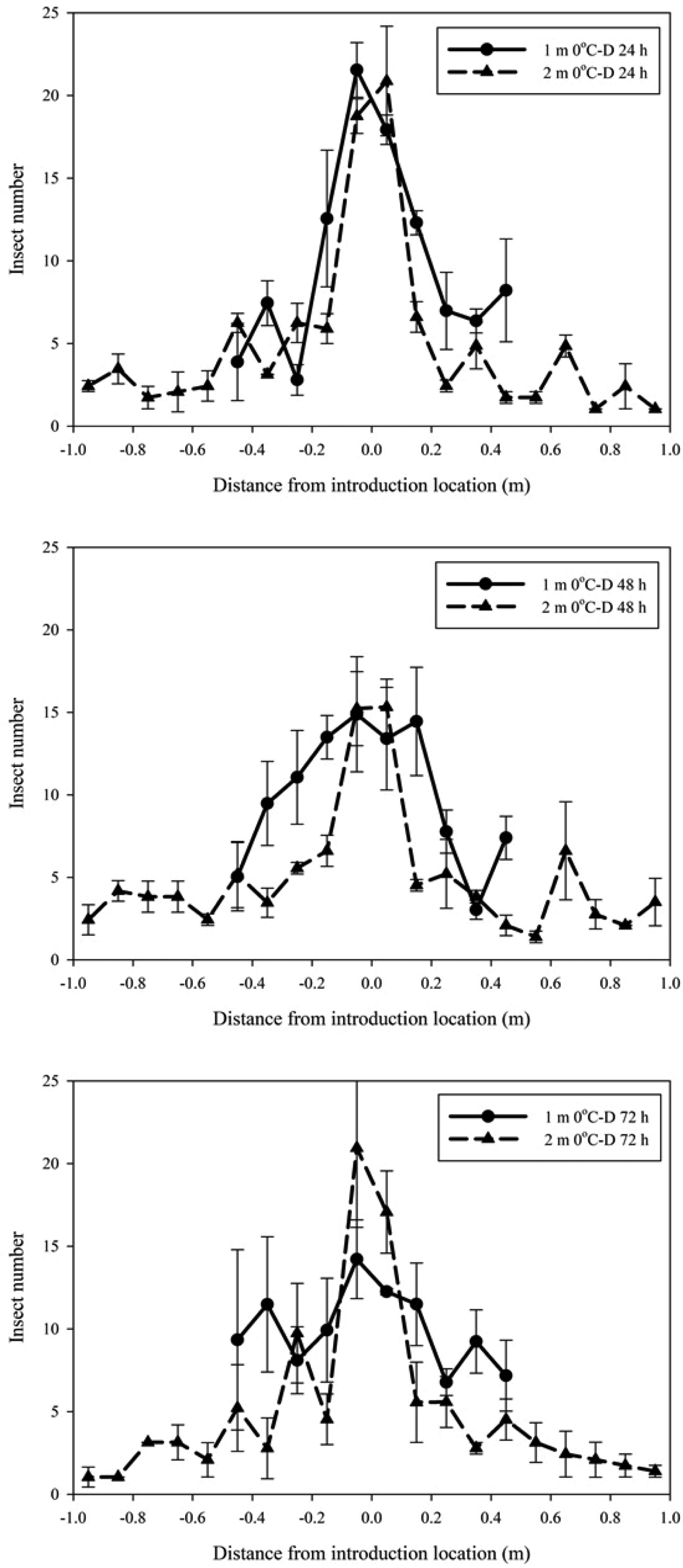

Fig. 3. Movement and distribution of *C. ferrugineus* adults under condition of no temperature differences in 1- and 2-m grain columns in different time periods. In the legend, 1 or 2 m is the grain column length. The number after 1 or 2 m is the nominal temperature difference between the two ends of the column, and number before h is the time after adult introduction (all data are presented as Mean ± SE, $n = 3$).

temperature in the sections with Negative Distance had a less influence because these sections were far from the water bath (Fig. 2; Table 1) than that at the Positive Distance. The water bath temperature influenced only certain distance of 0.45 to 0.25 m in 1- or 2-m columns except at 20°C-D. For the experiment at 20°C-D, the wheat temperature in the entire 1 m column increased after 24 h, which generated the highest temperature increase at the cold end (Negative Distance).

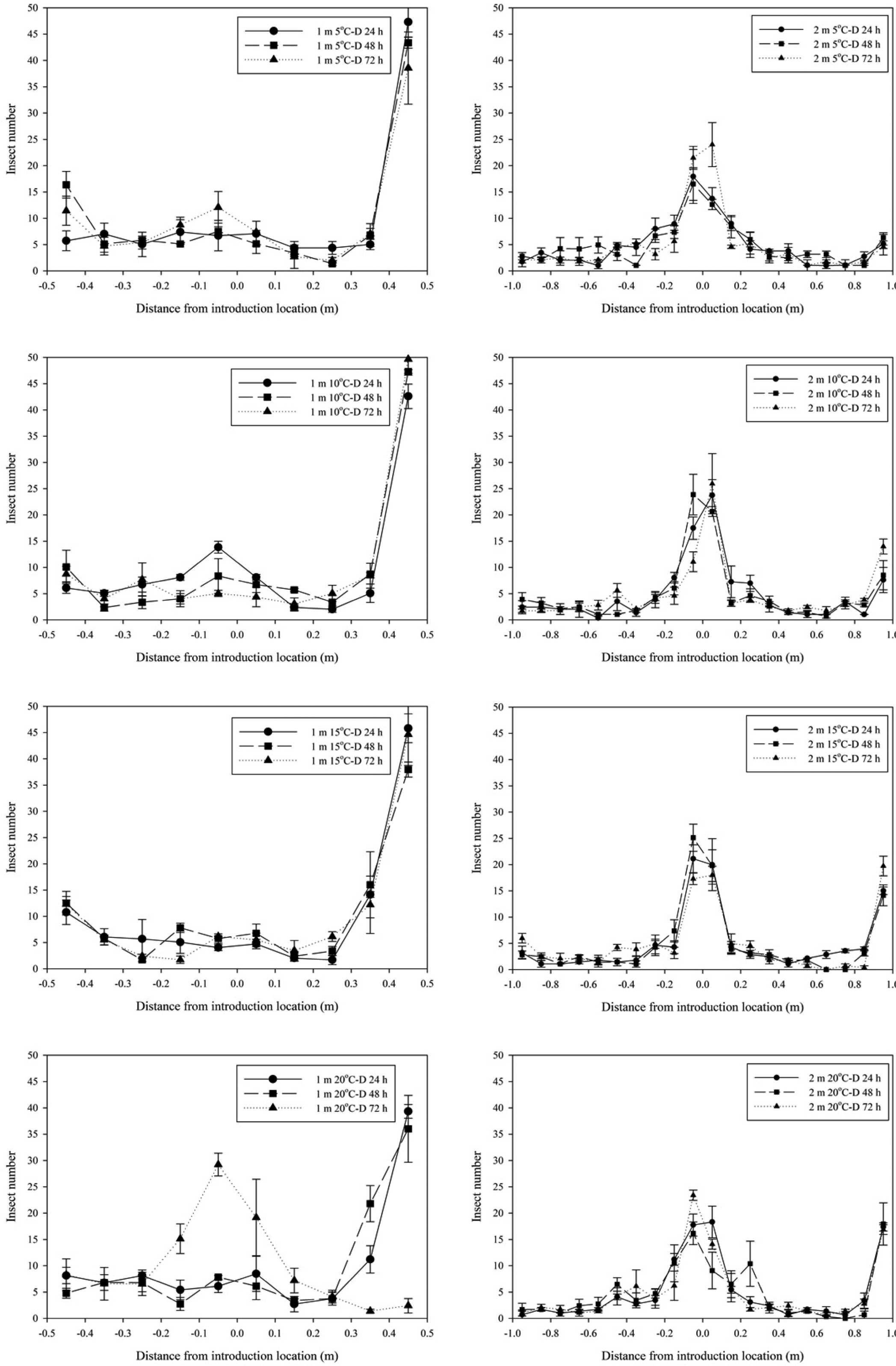

Fig. 4. Movement and distribution of *C. ferrugineus* adults in different times and under different temperature differences in 1- and 2-m grain columns. In the legend, 1 or 2 m is the grain column length. The number after 1 or 2 m is the nominal temperature difference between the two ends of the column, and number before h is the time after adult introduction (all data are presented as Mean ± SE, $n = 3$).

Movement in Column Without Temperature Difference

About 20% of adults were recovered from the sections at 0.05 and −0.05 m in 24 h in 1- and 2-m columns without temperature difference (Fig. 3). Figure 3 also clearly showed that rest of beetles dispersed towards both ends of the column with the increase of time. They were more evenly distributed in the columns when movement period increased from 24 to 72 h (Fig. 3), which showed a diffusion

Table 1. Temperature differences used for measuring movement and distribution of *C. ferrugineus* adults in 1- and 2-m columns filled with 12.5% moisture content wheat in 24, 48, or 72 h of movement period

	Temperature at warm end (°C)		Temperature difference along the column (°C)[b]							
	1 m column	2 m column	1 m column		2 m column		1 m column		2 m column	
Experiment[a]			ΔT_{cw1}[c]	ΔT_{cc1}[d]	ΔT_{cw2}[e]	ΔT_{cc2}[f]	ΔT_{mw1}[g]	ΔT_{mc1}[h]	ΔT_{mw2}[i]	ΔT_{mc2}[j]
0°C-D 24 h	20 ± 0	20.2 ± 0	0.1 ± 0	0.3 ± 0.2	0.1 ± 0	0.2 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.1
0°C-D 48 h	20.1 ± 0	20 ± 0	0 ± 0	0 ± 0	0.1 ± 0.1	0.1 ± 0.1	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0
0°C-D 72 h	20.2 ± 0	20 ± 0	0 ± 0	0 ± 0.1	0.1 ± 0	0.1 ± 0	0 ± 0	0 ± 0	0.1 ± 0	0.2 ± 0
5°C-D 24 h	26.3 ± 0.4	27.1 ± 0.2	6 ± 0.6	0.7 ± 0.7	6.5 ± 0.2	0.1 ± 0.2	4.9 ± 0.6	0.2 ± 0	6.3 ± 0.1	0 ± 0.1
5°C-D 48 h	27.3 ± 0.1	27.2 ± 0.2	7.3 ± 0.3	0.7 ± 0.8	6.8 ± 0.1	0.3 ± 0	6 ± 0.4	0.2 ± 0	6.5 ± 0.1	0.2 ± 0
5°C-D 72 h	27.2 ± 0.2	26.8 ± 0.1	6.7 ± 0.1	1.2 ± 0.9	6.6 ± 0.1	0.2 ± 0	5.3 ± 0.1	0.1 ± 0	6.3 ± 0.1	0.1 ± 0
10°C-D 24 h	30.7 ± 0	30.1 ± 0.4	10.5 ± 0	0.8 ± 0.9	9.5 ± 0.4	0 ± 0.1	9.1 ± 0.2	0.1 ± 0	9.4 ± 0.3	0.1 ± 0.1
10°C-D 48 h	31.3 ± 0	30.6 ± 0.2	10.6 ± 0.1	1.1 ± 0.9	10 ± 0.1	0.3 ± 0	8.3 ± 0.3	0 ± 0	9.4 ± 0	0.2 ± 0.1
10°C-D 72 h	30.9 ± 0.1	29.8 ± 0.2	10.2 ± 0.1	1.1 ± 0.8	9.2 ± 0.3	0.2 ± 0.1	8.1 ± 0.2	0 ± 0	8.9 ± 0.1	0.2 ± 0
15°C-D 24 h	34.6 ± 0.3	33 ± 0.3	14 ± 0.2	0.9 ± 0.7	12.2 ± 0.2	0.2 ± 0.1	11.2 ± 0.2	0.1 ± 0	12 ± 0.2	0.1 ± 0.1
15°C-D 48 h	34.2 ± 0.3	33.9 ± 0.9	13.4 ± 0	1.1 ± 0.8	13.3 ± 0.8	0.2 ± 0	10.9 ± 0.2	0 ± 0	12.8 ± 0.9	0 ± 0.2
15°C-D 72 h	35 ± 0.2	34.1 ± 0.4	14.2 ± 0	1 ± 0.9	13.8 ± 0.3	0.4 ± 0.1	11.8 ± 0.3	0 ± 0.1	13.4 ± 0.2	0.3 ± 0.1
20°C-D 24 h	37.5 ± 0.4	37.3 ± 0.5	6.8 ± 0.5	1 ± 0.8	16.7 ± 0.4	0.3 ± 0	14.2 ± 0.9	0 ± 0	16.1 ± 0.4	0.2 ± 0
20°C-D 48 h	38.5 ± 0.3	37.8 ± 0.6	16.6 ± 0.7	1.6 ± 0.5	16.8 ± 0.4	0.1 ± 0.3	13.2 ± 0.7	0.2 ± 0	16 ± 0.2	0 ± 0.2
20°C-D 72 h	44.7 ± 0.6	37.7 ± 0.4	5.5 ± 0.4	5.3 ± 0.3	16.9 ± 0.3	0.1 ± 0	3.6 ± 0.4	6 ± 0.5	16.4 ± 0.2	0 ± 0

[a]Number before °C-D is the nominal temperature difference between the warm and cold ends. Temperature at the cold end of the 1- and 2-m grain columns was the same as that of the environmental chamber set at 20°C. To increase the temperature on warm end, the water bath temperature was set at total of cold end temperature plus nominal temperature difference plus 5°C. All data are presented as Mean ± SE, $n = 3$.

[b]Temperature difference is represented as ΔT.

[c]Temperature difference from middle of the column to warm end in 1 m column, $\Delta T_{cw1} = T_{0.45} - T_0$.

[d]Temperature difference from middle of the column to cold end in 1 m column, $\Delta T_{cc1} = T_{-0.45} - T_0$.

[e]Temperature difference from middle of the column to warm end in 2 m column, $\Delta T_{cw2} = T_{0.95} - T_0$.

[f]Temperature difference from middle of the column to cool end in 2 m column, $\Delta T_{cc2} = T_{-0.95} - T_0$.

[g]Temperature difference from the midpoint of half column to warm end in 1 m column, $\Delta T_{mw1} = T_{0.45} - T_{0.25}$.

[h]Temperature difference from the midpoint of half column to cool end in 1 m column, $\Delta T_{mc1} = T_{-0.45} - T_{-0.25}$.

[i]Temperature difference from the midpoint of half column to warm end in 2 m column, $\Delta T_{mw2} = T_{0.95} - T_{0.55}$.

[j]Temperature difference from the midpoint of half column to cool end in 2 m column, $\Delta T_{mc2} = T_{-0.95} - T_{-0.55}$.

T0, T0.25, T-0.25, T0.45, T-0.45, T0.55, T-0.55, T0.95, and T-0.95 are the temperatures at 0, 0.25, −0.25, 0.45, −0.45, 0.55, −0.55, 0.95, and −0.95 m distance from the introduction location, respectively.

pattern (Campbell et al. 2006). Insect movement farther than 0.5 m from the insect introduction location in the 2-m column was small (Fig. 3), implying limited insect movement to farther locations during the studied periods.

Movement Under Temperature Differences

Adults had a biased movement to warmer sections in columns with temperature differences. This bias movement was more obvious in 1-m columns than that in 2-m column (Fig. 4). In the same length of the grain column, there were no significant difference of the adult distribution under different temperature differences (Table 2). In any movement period, more than 40% of adults moved to the warmer end of the 1-m column, whereas less than 15% of adults moved to the warmer end of the 2-m column. The maximum temperature gradients were located at the warmer end of the wheat column in both 1- and 2-m columns except 20°C-D in 1-m column (Fig. 2). In the experiment of 20°C-D in 1-m column, the maximum temperature gradient was located at the warmer end of the wheat column by 48 h (Fig. 2), and more than 40% of adults already moved to the warmest location by 48 h (Fig. 4). Therefore, more than 40% of adults preferred warmer locations and could detect the temperature difference in less than 0.5 m. When the maximum temperature gradient was located far (more than 0.8 m as in 2-m grain column), most adults (more than 95%) could not detect the temperature difference (Fig. 4).

When the water bath was higher than 45°C, beetles were found close to the top surface of wheat at the 0.45 and 0.95 m distance in 1- and 2-m columns, respectively. This was due to high temperature effect of the water bath. Jian et al. (2002) reported adults preferred temperature from 30 to 36.5°C, but adults moved away when temperature was higher than 42°C. Our result confirmed this phenomenon.

Movement Under Temperature Differences in Different Times

The increase in movement time could provide enough time for adults to move and respond to temperature differences. However, there was no significant difference (KS test; Table 2; Fig. 4) of the insect distribution in 1- or 2-m columns among different movement periods regardless of the temperature differences. These results indicated that adults could detect temperature difference in less than 24 h and would stay at the warmer locations once they found the warmer location.

Discussion

We found that the wheat temperature in the entire 1 m wheat column increased after 24 h only at the 20°C difference. Similar increase in temperature was not observed in 2-m column. We assumed it was

Table 2. Results of two-sample location tests and KS statistics of *C. ferrugineus* adult movement under different experimental conditions

Comparison of experiments[a]			Wilcoxon[b]		Median[b]		KS[b]	
			χ^2	$P > \chi^2$	χ^2	$P > \chi^2$	K_{sa}	$P > K_{sa}$
1 m grain column	5°C-D 72 h	10°C-D 72 h	37.36	0.0071*	27.11	0.1019	2.816	0.363
	10°C-D 72 h	15°C-D 72 h	37.08	0.0078*	26.98	0.1050	3.011	0.388
	15°C-D 72 h	20°C-D 72 h	44.39	0.0008*	32.66	0.0263*	3.265	0.421
	5°C-D 24 h	5°C-D 48 h	33.34	0.0219*	27.80	0.0873	2.768	0.357
	5°C-D 48 h	5°C-D 72 h	43.86	0.001*	31.397	0.0365*	3.119	0.402
	10°C-D 24 h	10°C-D 48 h	46.18	0.0005*	39.18	0.0042*	3.306	0.426
	10°C-D 48 h	10°C-D 72 h	35.77	0.0113*	27.25	0.0988*	2.932	0.378
	15°C-D 24 h	15°C-D 48 h	45.54	0.0006*	38.02	0.0059*	3.224	0.416
	15°C-D 48 h	15°C-D 72 h	44.92	0.0007*	30.15	0.0499*	3.211	0.414
	20°C-D 24 h	20°C-D 48 h	39.19	0.0042*	35.40	0.0125*	3.000	0.387
	20°C-D 48 h	20°C-D 72 h	44.02	0.0009*	40.01	0.0033*	3.211	0.414
2 m grain column	5°C-D 72 h	10°C-D 72 h	80.68	<0.0001*	67.90	0.0028*	4.257	0.388
	10°C-D 72 h	15°C-D 72 h	91.21	<0.0001*	73.92	0.0006*	4.393	0.401
	15°C-D 72 h	20°C-D 72 h	86.90	<0.0001*	73.86	0.0006*	4.508	0.411
	5°C-D 24 h	5°C-D 48 h	86.852	<0.0001*	74.04	0.0006*	0.409	4.487
	5°C-D 48 h	5°C-D -72h	85.91	<0.0001*	75.19	0.0004*	0.394	4.316
	10°C-D 24 h	10°C-D 48 h	89.38	<0.0001*	76.68	0.0003*	0.401	4.396
	10°C-D 48 h	10°C-D 72 h	85.57	<0.0001*	70.85	0.0014*	0.393	4.311
	15°C-D 24 h	15°C-D 48 h	92.02	<0.0001*	74.85	0.0005*	0.397	4.350
	15°C-D 48 h	15°C-D 72 h	98.34	<0.0001*	76.91	0.0003*	0.416	4.56
	20°C-D 24 h	20°C-D 48 h	95.20	<0.0001*	88.38	<0.0001*	0.437	4.788
	20°C-D 48 h	20°C-D 72 h	84.22	<0.0001*	74.46	0.0005*	0.407	4.463

[a]The number before '°C-D' is the nominal temperature difference in the grain column. The number before 'h' is the time after adult introduction (h). All data are presented as Mean ± SE, $n = 3$.
[b]Statistical test at $\alpha = 0.05$.

caused by the convection effect in the column when water bath temperature was higher than 40°C (Fig. 2). The heat transfer takes place from copper plate to grain column by both conduction and convection. Convection transfers heat faster when temperature is higher than the low end temperature. The heat transfer by convection is also influenced by the distance of the heat transfer. Convection heat transfer is mostly effective in short distance (Bergman et al. 2018). These two convection phenomena resulted in the grain temperature increase in the entire 1-m grain column, whereas only part of the grain increased its temperature in the 2-m grain column (Fig. 2).

This study found a diffusion pattern in wheat columns without temperature differences. Random movement could result in diffusion distribution. Therefore, our results confirmed the wandering movement behavior of the adults of C. *ferrugineus* as reported in literature (Anukiruthika et al. 2021). Adults of rusty grain beetles move to grain with 10% CO_2 concentration and wet grain (Parde et al. 2004) and avoid higher than 42.5°C grain area (Jian et al. 2002). Their vertical movement and distribution are significantly affected by the dockage percentage. The movement decreased with higher dockage (10%) when compared with 5% dockage; however, there is no bias movement observed in the horizontal columns. Adults respond to both temperature and moisture differences in stored wheat differently. Adults prefer warmer locations. Faster movement is observed at 12.5% m.c. than at 14.5% m.c. (Jian et al. 2005a). The sex of adults does not affect the adult movement (Jian et al. 2004a) but age and temperature acclimation of adults significantly influence the insect movement (Jian et al. 2005c). Our study had the similar result of *C. ferrugineus* movement as reported by Jian et al. (2002, 2004a) under linear temperature gradient in 1-m grain column. About 40% of beetles preferred the warmer end and showed a net displacement of 0.45 m regardless of variations in the temperature differences in 1-m column in the tested movement times. Therefore, adults of C. *ferrugineus* under linear temperature gradient had a similar response as that under nonlinear temperature differences.

Increasing temperature differences in 1- or 2-m columns had no effect on insect movement and distribution, and the grain column length influenced the insect distribution. These results might indicate that adult movement might be a combination of random and biased movement (Semeao et al. 2013). When adults could not detect the temperature difference, they had a random/wandering movement, whereas there was a bias movement after they detected the temperature difference. The lowest temperature difference in our study was for 5°C-D in 1-m column where the adults could actively move towards warmer sections of column with a transformation from random to biased movement. The present study could be extended to the vertical grain columns in future to find whether the movement and distribution of the beetles are the same under nonlinear temperature differences as that of distribution pattern under linear temperature gradients as reported in literature (Jian et al. 2004b, 2005a, 2005b).

The movement and distribution of adults of *C. ferrugineus* are mainly influenced by temperature (Jayas et al. 1994). Even though adults of *C. ferrugineus* had a positive temperature response, adults could only detect the temperature difference in about 0.5 m and only 40% of adults moved to the warmer sections. These results imply that not all insects may move to the warmer center in stored grain bins (Jayas et al. 1994). Thus, this conclusion should be considered during insect pest management. For example, insect traps might not detect adults that are located more than 0.5 m away from the trap considering temperature as driving factor rather than semiochemicals in traps. The result of this study also provides a valuable insight for developing mathematical model of insect movement and distribution under different temperature differences and time periods in stored grain bins. These results confirm that temperature is one of significant driving forces for insect movement in consideration with the length of grain column. Thus, the research findings of this work could help in deciding the size of finite elements or control volumes to be less than 0.5 m during mathematical modeling of 3D insect movement and distribution in stored grains.

Considering these aspects, the future direction of work should focus on determining the moisture response of insects in relation to the length of grain column to know how far the beetles could sense the moisture difference in a grain column. The present study focused on movement behavior of *C. ferrugineus* by considering its vast occurrence and significance of damages caused in stored wheat (Hagstrum et al. 2012, Nayak and Daglish 2018). Further, the same study can be extended to other stored product insects such as *T. castaneum*. The synergistic or antagonistic effects on insect movement should be also studied by having temperature and moisture differences in the same and opposing directions, respectively, as are expected in full size bins.

The results of our study showed that grain column length is a significant factor affecting insect movement and distribution along with temperature differences and movement period. This indicated that adults could not detect warmer location which is 0.9 m far away, while they could detect the warmer location which is less than 0.5 m. This might explain that not all insects move to warmer center in a grain bin during winter (Flinn et al. 2010).

On comparing the results of both 1- and 2-m grain columns, the following conclusions are drawn.

- Higher than 5°C temperature difference in 0.5 m could be readily detected by adults in 24 h.
- The temperature response of beetles diminished with increasing grain column length from 1 to 2 m. Adults could not detect warmer grain located at 0.9 m away.
- About 40% adults moved to the warmer grain located in less than 0.5 m.

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