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Influence of landscape pattern in flour residue amount and distribution on *Tribolium castaneum* (Herbst) response to traps baited with pheromone and kairomone

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ABSTRACT

Tribolium castaneum (Herbst), the red flour beetle, is a major pest of food facilities and is typically monitored using traps that capture walking individuals. In flour mills the accumulation of residues of flour on surfaces has the potential to influence beetle movement and response to trap attractants. Different flour residue landscapes of habitat (flour) within a matrix of no flour with the following characteristics were created: low abundance (10% coverage) and fragmented distribution, high abundance (30% coverage) and fragmented distribution, low abundance and clumped distribution, high abundance and clumped distribution, 0% coverage, and 100% coverage. Response of individual beetles to traps placed on top of these landscapes was evaluated; traps were either baited with aggregation pheromone and kairomone or contained no attractants. Encounters with the two types of traps were not significantly different for any of the specific landscapes, but greater numbers tended to encounter traps with attractants on fragmented landscapes and 100% flour landscapes. Combining landscape types, the proportion of beetles encountering pheromone + kairomone-baited traps (0.61) was not greater than the proportion encountering empty traps (0.50). However, when combining just the fragmented landscapes there was a significantly greater response to traps with attractants (78%) than traps without (50%), but no difference in response on the combined clumped landscapes. Movement pathways, analyzed using video recordings of beetles, showed a general trend for 0% and 100% habitat landscapes to be most different from each other and 10% and 30% habitat landscapes tended to group together, but only for maximum distance traveled in an interval, velocity, and mean turn angle were significant differences observed. Results suggest that fragmented landscapes may have some impact on beetle response to attractants, but a potential mechanism for this needs further evaluation.

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1. Introduction

Tribolium castaneum (Herbst), the red flour beetle, is a major pest of food facilities, such as mills, manufacturing plants, warehouses, and retail stores (Campbell et al., 2010). Traps used to monitor *T. castaneum* inside food facilities are typically pitfall designs that capture walking individuals and are baited with aggregation pheromone and food-based kairomone lures (Burkholder, 1990; Chambers, 1990; Mullen, 1992; Phillips, 1997; Phillips et al., 2000; Campbell, 2012). How *T. castaneum* respond to commercially available traps and attractants may be influenced by the landscape of physical and environmental conditions at the

locations where traps are placed inside a food facility. Semeao et al. (2012) found that trap locations within a flour mill with larger captures tended to have greater flour dust accumulation, higher temperatures, and closer proximity to milling equipment. Romero et al. (2009) found that *T. castaneum* movement patterns were influenced by the distribution pattern of flour accumulations. Presence of food in the environment has also been shown to reduce *T. castaneum* captures in traps (Stejskal, 1995). These findings suggest that accumulation of food material such as flour on surfaces might influence how beetles interact with traps placed out to monitor them. If this is true it could influence the effectiveness of pheromone + kairomone-baited traps and impact how captures should be interpreted in different types of environments.

During milling and other manufacturing processes, fine particles of grain-based material can be produced and released into the air and these particles can settle and accumulate on surfaces. In





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addition, grain-based material can be released onto surfaces during equipment operation, mechanical failures, or cleaning, and result in spillage accumulations on surfaces. The milling of wheat kernels into flour is a process that especially tends to produce a large amount of flour dust and spillage, and accumulations of this material can be an important resource supporting populations of T. castaneum within flour mills. Housekeeping to remove these accumulations of food material at regular intervals is an important component of a food facility sanitation program, but at any given time surfaces may have a residue of food material. This food residue can directly impact insect captures since it can coat sticky surfaces or fill pitfall traps and therefore reduce trap efficacy. The development of covers for pitfall traps used in food facilities is a result of this issue. However, food residues may also indirectly impact captures in traps through their influence on insect movement (Romero et al., 2009) and nutritional status (Fedina and Lewis, 2007).

Landscape structure, the amount and distribution of a habitat type, can have an impact on an organism's foraging behavior. The residue of food material on surfaces within a food processing facility, which can be considered as habitat for T. castaneum, can have its own spatial structure of presence and absence and depth of accumulations (Semeao et al., 2012). Neutral landscape models have been used to investigate how T. castaneum respond to spatial pattern in habitat abundance and distribution, and shown that beetles move more slowly and tortuously as the individual patches of flour habitat change from clumped to fragmented in distribution and as a result beetles tend to remain longer within individual patches of flour and on landscape as a whole (Romero et al., 2009). Thickness of flour residue patches also influenced T. castaneum movement, particularly in terms of movement across patch edges and time spent in patches of flour (Romero et al., 2010). Given that flour residue pattern influences beetle movement, as revealed using neutral landscape models, it may also influence the probability of beetles encountering monitoring traps when placed in food facilities.

Walking T. castaneum exhibit a behavioral response to food and aggregation pheromone, and traps targeting walking individuals typically use a combination of these two types of attractants. The aggregation pheromone, 4,8-dimethyldecanal, is produced by feeding males and is attractive to both sexes (Suzuki, 1980; Suzuki et al., 1984). The pheromone occurs in four different forms and is released by males at a 4:4:1:1 [(4R,8R):(4R,8S):(4S,8R):(4S,8S)] ratio (Lu et al., 2011). Multiple studies have evaluated how T. castaneum, and Tribolium confusum Jacquelin DuVal which shares the same pheromone (Suzuki and Sugawara, 1979), respond to pheromone (Sokoloff, 1974; Ryan and O'Ceallachain, 1976; O'Ceallachain and Ryan, 1977; Levinson and Mori, 1983; Boake and Wade, 1984; Barak and Burkholder, 1985; Obeng-Ofori and Coaker, 1990; Obeng-Ofori, 1991; Lewis and Austad, 1994; Olsson et al., 2006; Verheggen et al., 2007; Duehl et al., 2011; Campbell, 2012). Tribolium castaneum and T. confusum also respond to food odors (Willis and Roth, 1950; Phillips et al., 1993), but attraction to flour appears to be negligible (Hughes, 1982; Romero et al., 2010). The response to pheromones by T. castaneum can be increased by addition of food odors, but the increase in response appears limited (Phillips et al., 1993; Campbell, 2012). However, these studies have only evaluated beetle response under simplified conditions where there was little potential for landscape features and competing attractants to influence the strength of the response.

The food volatile, gustatory, and physical cues associated with a landscape containing flour could impact *Tribolium* spp. response to pheromone and kairomone attractants in traps, but the nature of this impact is difficult to predict. Flour accumulations may enhance captures through the interaction of pheromone and food odors increasing attraction or through inducing a more tortuous search path that retains beetles in the vicinity of the trap. Alternatively, flour accumulation could reduce captures in traps by reducing probability of encounter either by presenting competing attractants or by limiting beetle dispersal distance. Campbell (2012) described an experimental approach for evaluating response to traps that provides a realistic evaluation of the strength of insect response under simulated field conditions. A modification of that approach is used here to assess how flour residue pattern influences beetle response to pheromone + kairomone-baited traps, using neutral landscape models of flour distribution originally developed by Romero et al. (2009). Still air conditions were used in this study, even though attraction to traps is stronger under moving air conditions (Campbell, 2012), so that results could be more directly compared to conditions in Romero et al. (2009) and because this represents conditions typical of trap locations in flour mills.

2. Materials and methods

Tribolium castaneum originally collected from a flour mill within two years of conducting the study, was maintained on wheat flour and brewers yeast (5% by weight) in an incubator set at 25 °C, 65% rh, and 14:10 light:dark cycle. Beetles between two and three weeks after adult emergence were collected for use in experiments. Beetles were transferred individually to 30 ml clear plastic cups (Jet Plastica Industries, Hatfield, PA) that contained flour and cracked wheat sufficient to just cover the bottom of the cup. Beetles were held for approximately 48 h in an incubator under conditions described above prior to start of experiments.

The experimental arena simulated the floor/wall junction along which traps are typically placed when used for monitoring. The arena consisted of a floor made from a 61 cm by 61 cm piece of particle board that had been spray painted white and a wall made from a piece of white laminated board (61 cm long \times 20 cm wide \times 1.5 cm thick). The smooth laminate coating on the wallboard prevented beetles from climbing. The floor was covered with a piece of white paper cut large enough to extend slightly over the sides of the floor. Then the wall was placed standing on its side perpendicular to the floor, and aligned along north edge of floor. Tape was used to mark off a 50 cm by 45 cm observation zone, with one 50 cm edge being the wall.

Different flour residue landscapes (50 \times 50 cm) of habitat (unbleached white flour) and matrix (no flour) developed in Romero et al. (2009) were used in this experiment. Experimental landscapes consisted of two grain sizes (2 \times 2 and 10 \times 10 cm) within two levels of habitat abundance (10 and 30% coverage of landscape), with four different random maps created for each abundance by grain size combination using RULE software program (Gardner, 1999). Holding the landscape extent constant while varving grain size produced landscapes with different degrees of habitat aggregation (i.e., fragmented and clumped), with specific landscape characteristics described in detail in Romero et al. (2009). Additional landscapes with 0% and 100% flour were also included in experiment. Heavy cardstock templates of each landscape pattern with cutouts for cells with flour were used to create these patterns of flour habitat patches (see Romero et al. (2009) for detailed description). The appropriate cardboard template for a given treatment was aligned next to the wall in the experimental area and centered within observation zone. Flour was applied evenly over the template and paper covering the floor to a depth of approximately 1 mm using a 60 mesh sieve to distribute the flour. The template was then removed to create the pattern of flour and matrix on the floor. Between each experimental replication the paper and flour were removed and replaced with a new piece of paper and a new flour landscape pattern.

In all experiments, insect response to either a Storgard[®] DomeTM trap with attractants (kairomone oil and pheromone lure for *T. castaneum*) (Trece, Adair, OK) or trap without attractants as a control was evaluated. Attractants were added to traps at least one day before the trial was to be conducted and the same pheromone lure and kairomone oil was used in multiple trials over a one-week period and then replaced. The trap was placed at the northeast corner of the observation zone and touching the wallboard.

Twelve treatment combinations were evaluated: traps with or without attractants combined with 0%, 10% and 30% fragmented $(2 \times 2 \text{ cm cells})$, 10% and 30% clumped (10 \times 10 cm cells), or 100% habitat landscapes. On a given day, twelve trials were performed with one replicate of each treatment combination, with the order of treatment combinations randomized. For each of the fragmented and clumped landscapes, one replicate of each landscape template (four patterns) and orientation (each side of the template flush with the wallboard) was performed. A total of 16 replicates were performed for each treatment combination, with one replicate performed per day. Environmental conditions were measured immediately before each replicate, with air temperature and relative humidity measured 1 cm and 4 cm above the floor surface, respectively, using a handheld weather meter (Kestrel 3000, Nielsen-Kellerman, Boothwyn, PA USA). An Atkins Series 396K thermometer (Atkins Technical, Gainesville, FL USA) was used to measure surface temperature. Mean environmental conditions during experiments were 24.8 \pm 0.1 °C air temperature, 24.8 \pm 0.1 °C surface temperature, and 27.2 \pm 0.3% rh.

Beetles were released, one per replicate, by placing a beetle in a glass 3.7 ml vial and upending the vial at the midpoint of the observation area and approximately 2 cm away from the wall. This release distance was 15 cm from the edge of the trap. The beetles were left confined within the upended vial for 3 min to acclimate. After this period, the vial was removed and beetles were observed until they left the observation area, encountered the trap, or a period of 5 min had expired. The outcome of each replicate was recorded so that proportion of beetles responding could be calculated. The sex of the beetles was determined after experiment, with results indicating that 105 females and 87 males were tested (sex ratio of 0.55). Campbell (2012) did not find a significant difference between sexes in response to attractants in traps.

All trials were video recorded from time of beetle release to observation termination so that movement pathways could be measured and analyzed. A video camera (XL1 Digital Video Camcorder with 16x Zoom XL 5.5–88 mm lens, Canon, Lake Success, NY USA) was attached to the arm of a stand and positioned pointing straight down at observation zone. The position of the camera was the same in all trials, and the field of view enabled the whole observation zone to be visible. For analysis, the analog recordings were converted using Studio Plus software (version 9.4.3, Pinnacle Systems, Mountain View, CA USA) into digital MPEG format files. The digital files were then imported into EthoVision 3.0 software (Noldus Information Technology, Leesburg, VA USA).

Within the EthoVision software, a rectangular area 50 cm long (with wall as one side) and 45 cm wide was defined using the tape marks on the boards as guides. This observation zone was the largest possible while still enabling reliable tracking of beetles. A point was defined at the center of the trap and used to determine the average distance of beetle from trap. The trap itself was defined as a hidden zone since beetles could not be observed after passing under the lid of the trap. For beetle detection the 'subtraction' setting was used, and objects darker than the background were detected using a minimum pixel size of 4 and maximum pixel size of 40. A scan window was used with the default settings, and the option of searching the whole window was selected. The option to use the last measured position when the software could not detect beetle at a given time point was selected in EthoVision. Once program was determined to be tracking reliably in the preview mode, the paths were measured and analyzed. The following metrics were calculated for each replicate: average distance from the trap (cm), total distance traveled (cm), maximum distance traveled in an interval (cm), velocity (cm/s), heading (degrees), mean turn angle (degrees), mean angular velocity (degrees/s), relative meander (degrees/cm). Relative meander is a measure of the signed direction of turning per unit distance and ranges from –180 to 180 degrees/cm.

Proportion of individuals encountering trap and leaving the observation zone were compared among treatments using contingency table analysis and chi-square tests (Zar, 1999). Differences in movement pathway metrics were evaluated using General Linear Models (GLM) procedure and Ryan-Einot-Gabriel-Welsch multiple range test (SAS software v. 9.2, SAS Institute, Cary NC).

3. Results

Most beetles found the trap or left the observation zone during the 5 min observation period, with beetles remaining in the observation zone only if there was flour present (Fig. 1). Encounters with traps with attractants compared to traps without attractants were not significantly different for any of the specific landscape treatments (chi-square tests, P > 0.05), but a greater number of



Fig. 1. The number of individual *Tribolium castaneum* captured in trap with or without attractants (pheromone and kairomone), that leave observation zone, or remain in observation zone for a 5 min period on different landscape patterns of flour deposition (0, 10, 30, or 100% coverage with flour and fine or course grain cell sizes to create clumped or fragmented distributions of the 10 and 30% flour coverage landscapes).

beetles tended to encounter traps with attractants on the fragmented landscapes and the 100% flour landscapes (Fig. 1). These two landscapes are functionally similar to each other based on earlier research by Romero et al. (2009). For the combined landscape types, the proportion of insects encountering traps baited with pheromone and kairomone (0.61) was not greater than the proportion encountering empty control traps (0.50) ($\chi^2 = 2.11$, d.f. = 1, P = 0.146).

Grouping the data by grain size and habitat amount, revealed that only fragmentation had an influence on response to trap. On the fragmented landscapes there was a significantly greater response to traps with (78%) than traps without (50%) attractants $(\chi^2 = 4.344, d.f. = 1, P = 0.037)$, but not on the clumped landscape (53% versus 53%; $\chi^2 = 0.063$, d.f. = 1, P = 0.802). Combining replicates with and without attractants in traps, there was no difference in percentage finding the trap between fragmented and clumped landscapes ($\chi^2 = 1.159$, d.f. = 1, P = 0.282). There was not a significant difference between traps with and without attractants when data were grouped by habitat amount: 10% (66% versus 47%; $\chi^2 = 1.587$, d.f. = 1, P = 0.208) or 30% (66% versus 56%; $\chi^2 = 0.263$, d.f. = 1, P = 0.608) abundance. Combining replicates with and without attractants, there was no difference in percentage finding the trap between two habitat abundances ($\chi^2 = 0.129$, d.f. = 1, P = 0.720).

For the pathway metrics using combined traps with and without attractants, the general trend was that the 0% and 100% landscapes tended to be the most different from each other and the 10% habitat and 30% habitat landscapes tended to group together, with fragmentation levels appearing to be less important. However, only for maximum distance traveled in an interval, velocity, and mean turn angle were significant differences observed (Table 1). Maximum distance traveled in an interval is a useful metric given the variation in rate of movement that can occur as organisms move between matrix and habitat. The shortest mean maximum distance was on the 100% habitat landscape (which was not different from the 10% clumped), but there was considerable statistical overlap among the different landscapes and none of the fragmented or clumped landscapes were statistically different from the 0% habitat landscape. For velocity, the fastest mean velocity occurred on the 0% habitat landscape and the slowest on the 100% habitat landscape, with considerable overlap among the velocities on the different fragmented and clumped landscapes. For mean turn angle, there was considerable statistical overlap among the different landscapes, but with smallest turn angles on the 0% habitat landscape, which has no habitat edges, and largest turn angles on the 30% fragmented landscape, which has the largest amount of habitat edges.

There were also no significant differences for any of the movement pathway metrics, between fragmented landscapes (combined 10% and 30%) with and without attractants in the traps (*t*-test or Mann–Whitney rank sum test, P > 0.05) even though in earlier analysis trap encounters were significantly greater. There were also no differences between treatments with and without attractants on the combined clumped landscapes (*t*-test or Mann–Whitney rank sum test, P > 0.05). Combining the traps with and traps without attractants, none of the pathway metrics differed between the fragmented and clumped landscapes or between the two habitat abundance landscapes (*t*-test or Mann–Whitney rank sum test, P > 0.05), except that the maximum distance moved in an interval was greater on the 30% coverage (0.61 ± 0.02 cm) than the 10% coverage (0.53 ± 0.02 cm) landscapes based on a Mann–Whitney rank sum test (U = 1434, d.f. = 1, P = 0.007).

4. Discussion

Landscape structure has been shown to impact the ability of an organism to successfully search for resources (With and Crist, 1995; With and King, 1999; With et al., 2002). Typically research has focused on how landscape structure influences how resource patches are interconnected (Taylor et al., 1993; Wiens et al., 1997; Moilanen and Hanski, 2001), but landscape structure could also influence the probability of successfully encountering point sources of attractants (e.g., pheromone- or kairomone-baited trap, calling female, host). Landscape influences are not typically considered when evaluating an insect's ability to find baited traps, but in cases where they have been investigated, landscape pattern has influenced captures. For example, the number of mosquitoes caught in dry ice-baited traps was influenced by spatial pattern in bloodmeal hosts and vegetation (Lothrop and Reisen, 2001: Thiemann et al., 2011). Understanding how the landscape where a trap is placed influences insect response could improve the implementation and interpretation of monitoring programs.

In interior landscapes in which stored-product insects are monitored using traps, the physical and environmental landscape can vary considerably among trap locations and specific features have been shown to impact insect captures. Horizontal surfaces can increase captures of flying individuals responding to sex pheromone-baited traps, presumably by providing surfaces for landing prior to entering the trap (Campbell et al., 2002; Nansen et al., 2004). For walking T. castaneum, landscape features such as vertical edges have been shown to influence behavior (Campbell and Hagstrum, 2002). Semeao et al. (2012) measured physical and environmental features associated with trap locations and their relationship with T. castaneum captures in a commercial flour mill. Variation in captures among locations and a significant relationship between insect capture and flour dust accumulation was found. Movement behavior of T. castaneum has also been shown to be influenced by the distribution of flour resources (Naylor, 1961; Lavie and Ritte, 1978; Campbell and Hagstrum, 2002; Campbell and Runnion, 2003; Romero et al., 2009). The relatively weak attraction

Table 1

	Movement pathway	metrics for individual	<i>castaneum</i> adults on different	it landscape types contai	ining traps with and	d without attractants.
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Landscape	Mean distance from trap (cm)	Total distance traveled (cm)	Maximum distance traveled in an interval (cm)	Velocity (cm/s)	Heading (degrees)	Mean turn angle (degrees)	Mean angular velocity (degrees/sec)	Relative meander (degrees/cm)
0%	23.1 ± 1.5	46.7 ± 6.6	0.57 ± 0.02 ab	0.9 ± 0.1 a	202.6 ± 18.1	$42.9\pm3.2~b$	-46.9 ± 13.7	-86.4 ± 27.5
10% fragmented	20.1 ± 1.3	62.9 ± 10.1	0.57 ± 0.03 ab	$0.7\pm0.0\ abc$	$\textbf{228.8} \pm \textbf{16.6}$	$43.7 \pm 4.0 \text{ ab}$	-58.9 ± 10.4	-92.9 ± 18.1
10% clumped	21.7 ± 1.3	55.7 ± 6.5	$0.49\pm0.03~bc$	$0.8\pm0.0\;ab$	203.0 ± 19.8	$42.9\pm3.2~ab$	-48.0 ± 10.4	-86.6 ± 19.4
30% fragmented	19.8 ± 1.1	$\textbf{78.6} \pm \textbf{9.2}$	$0.58\pm0.03~ab$	$0.7\pm0.0\ bc$	235.5 ± 17.2	$57.1\pm5.1~\text{a}$	-75.1 ± 17.4	-131.3 ± 32.4
30% clumped	19.6 ± 1.3	$\textbf{70.8} \pm \textbf{8.7}$	$0.63\pm0.03~a$	$0.7\pm0.0\ abc$	219.7 ± 20.1	$53.6\pm4.5~ab$	-71.5 ± 14.4	-117.0 ± 24.5
100%	21.0 ± 1.2	59.1 ± 7.5	$0.46\pm0.03\ c$	$0.6\pm0.0\;c$	202.5 ± 20.9	$54.0\pm4.9~ab$	-62.6 ± 13.3	-111.4 ± 24.7
GLM analysis								
F	1.04	1.90	4.89	3.70	0.62	3.22	0.75	0.55
d.f.	5, 186	5, 183	5, 184	5, 183	5, 182	5, 182	5, 182	5, 182
Р	0.3937	0.0969	0.0003	0.0032	0.6837	0.0082	0.5886	0.7359

to volatile aggregation pheromone and kairomone cues under still air conditions (Campbell, 2012) and weak response to flour volatiles, but a strong response to flour patch edges (Romero et al., 2009; Romero et al., 2010), suggests that the physical landscape of flour residues may influence encounters with traps.

In the current study, overall there was no increase in trap encounters with the presence of attractants in the trap, which is consistent with earlier findings under still air conditions (Campbell, 2012). However, increased response to traps with attractants compared to those without was observed on the fine-grained or fragmented landscapes: a trend for more encounters on the individual landscapes, particularly on the 30% habitat and fragmented landscape, and a significant increase when the two habitat abundance levels were combined. Movement pathway metrics were not significantly different on the fragmented landscapes compared to the clumped landscapes. However, although not significant, turn angles and meander tended to be greatest on the fragmented landscapes. Thus, there was not a detectable behavioral change in their movement pathways that might generate this difference in trap encounters on fragmented landscapes.

There are physical differences among the landscape types used in this study that were previously found to be associated with changes in beetle behavior. For example, Romero et al. (2009) reported that there was a 20-fold increase in the number of habitat patches in fragmented landscape compared to the clumped landscape. As landscapes became more fragmented and habitat abundance increased, landscapes had significantly more edges and distance between patches decreased. Beetles moving in fragmented landscapes encountered a high number of edges and did not travel as far between edge encounters. This resulted in beetles that traveled at a slower rate and had a more complex movement pathway. However, in the current study, significant differences in the movement pathway metrics were not observed between different levels of fragmentation and abundance, where differences occurred typically the 100% flour landscape was different from other treatments. Differences between the current and the earlier Romero et al. (2009) study might be due to the longer time frame of the observations, different arena used, or the more detailed path metric analysis used.

While, as discussed above, encounters with traps with attractants were greater than traps without attractants on fragmented landscapes, encounters with traps without attractants appeared more similar among the different landscape patterns. Given the small active space under still air conditions reported in Campbell (2012), landscape influences on trap encounters were predicted to be similar regardless of attractants. The lack of significant influence of landscape fragmentation on movement pathway metrics, suggests that fragmented landscapes may be either influencing how beetles respond to the volatile attractants rather than just physically changing their movement pathways, or generating changes in movement pathways that were not detectable in the current analysis. A beetle's perception of fragmentation may lead to a change in its response to aggregation pheromone, although the specific mechanism for this is not apparent. Tribolium castaneum does adjust patterns of oviposition in response to spatial pattern in resource (Campbell and Runnion, 2003; Romero, 2007), indicating that they can perceive differences in landscape structure and adjust behavioral responses other than just movement. Alternatively, differences in movement pathways may have occurred but were not detected either because individual variation covered up differences or changes in behavior resulting in differences in trap encounters may have only been expressed in close proximity to the trap. For example, the fragmented landscapes would be more likely to have flour edges close to the trap than clumped landscapes. The potential mechanism for this increased response to attractants needs further evaluation.

The results of this experiment indicate that flour residue pattern had some influence on response to traps, primarily due to increased trap encounters on fragmented landscapes. However, overall the impacts of the flour landscapes were limited suggesting that this variable would not likely influence the detection of beetle activity. However, if additional variables such as flour thickness were incorporated it is possible that the effects would be greater since increasing the depth of the patch will impact tendency to enter and leave patches (Romero et al., 2010) and perhaps more strongly impact turn rates and probability of remaining in the observation zone around the trap. The practical implications of these findings relate to how sanitation activities within a food facility can potentially impact monitoring programs. Increasing sanitation will decrease the amount of food material available and make it more fragmented in distribution. The findings presented here and in earlier studies do indicate that abundance and fragmentation can influence rate of beetle movement and probability of encountering a trap and that the surrounding environment should be considered when evaluating insect response to traps. Further evaluation at larger spatial scales, longer exposure times, and including other variables such of air flow might reveal additional impacts not detectable using the current protocol.

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References

- Barak, A.V., Burkholder, W.E., 1985. A versatile and effective trap for detecting and monitoring stored-product Coleoptera. Agriculture, Ecosystems and Environment 12, 207–218.
- Boake, C.R.B., Wade, M.J., 1984. Populations of the red flour beetle *Tribolium cas-taneum* (Coleoptera: Tenebrionidae) differ in their sensitivity to aggregation pheromones. Environmental Entomology 13, 1182–1185.
- Burkholder, W.E., 1990. Practical use of pheromones and other attractants for stored-product insects. In: Ridgway, R.L., Silverstein, R.M., Inscoe, M.N. (Eds.), Behavior-modifying Chemicals for Insect Management: Applications of Phermones and Other Attractants. Marcel Dekker. Inc., New York. pp. 497–516.
- Campbell, J.F., Hagstrum, D.W., 2002. Patch exploitation by *Tribolium castaneum*: movement patterns, distribution, and oviposition. Journal of Stored Products Research 38, 55–68.
- Campbell, J.F., Runnion, C., 2003. Patch exploitation by female red flour beetles, *Tribolium castaneum*. Journal of Insect Science 3, 20. available online: insectscience.org/3.20.
- Campbell, J.F., Mullen, M.A., Dowdy, A.K., 2002. Monitoring stored-product pests in food processing plants: a case study using pheromone trapping, contour mapping, and mark-recapture. Journal of Economic Entomology 95, 1089–1101.
- Campbell, J.F., Toews, M.D., Arthur, F.H., Arbogast, R.T., 2010. Long-term monitoring of *Tribolium castaneum* in two flour mills: seasonal patterns and impact of fumigation. Journal of Economic Entomology 103, 991–1001.
- Campbell, J.F., 2012. Attraction of walking *Tribolium castaneum* adults to traps. Journal of Stored Products Research 51, 11–22.
- Chambers, J., 1990. Overview on stored-product insect pheromones and food attractants. Journal of the Kansas Entomological Society 63, 490–499.
- Duehl, A.J., Arbogast, R.T., Teal, P.E., 2011. Age and sex related responsiveness of *Tribolium castaneum* (Coleoptera: Tenebrionidae) in novel behavioral bioassays. Environmental Entomology 40, 82–87.
- Fedina, T.Y., Lewis, S.M., 2007. Effect of *Tribolium castaneum* (Coleoptera: Tenebrionidae) nutritional environment, sex, and mating status on response to commercial pheromone traps. Journal of Economic Entomology 100, 1924– 1927.
- Gardner, R.H., 1999. RULE: map generation and spatial analysis program. In: Klopatek, J.M., Gardner, R.H. (Eds.), Landscape Ecological Analysis: Issues and Applications. Springer-Verlag, New York, pp. 280–303.
- Hughes, A.L., 1982. Attraction of adult *Tribolium confusum* to flour conditioned by male conspecifics. Behavioural Processes 7, 237–253.

- 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.
- Levinson, H.Z., Mori, K., 1983. Chirality determines pheromone activity for flour beetles. Naturwissenschaften 70, 190–192.
- Lewis, S.M., Austad, S.N., 1994. Sexual selection in flour beetles: the relationship between sperm precedence and male olfactory attractiveness. Behavioral Ecology 5, 219–224.
- Lothrop, H.D., Reisen, W.K., 2001. Landscape affects the host-seeking patterns of *Culex tarsalis* (Diptera: Culicidae) in the Coachella Valley of California. Journal of Medical Entomology 38, 325–332.
- Lu, Y., Beeman, R.W., Campbell, J.F., Park, Y., Aikins, M.J., Mori, K., Akasaka, K., Tamogami, S., Phillips, T.W., 2011. Anatomical localization and stereoisomeric composition of *Tribolium castaneum* aggregation pheromones. Naturwissenschaften 98, 755–761.
- Moilanen, A., Hanski, I., 2001. On the use of connectivity measures in spatial ecology. Oikos 95, 147–151.
- Mullen, M.A., 1992. Development of a pheromone trap for monitoring *Tribolium* castaneum. Journal of Stored Product Research 28, 245–249.
- Nansen, C., Phillips, T.W., Sanders, S., 2004. Effects of height and adjacent surfaces on captures of indianmeal moth (Lepidoptera: Pyralidae) in pheromone-baited traps. Journal of Economic Entomology 97, 1284–1290.
- Naylor, A.F., 1961. Dispersal in the red flour beetle, *Tribolium castaneum* (Tenebrionidae). Ecology 42, 231–237.
- Obeng-Ofori, D., Coaker, T.H., 1990. *Tribolium* aggregation pheromone: monitoring, range of attraction and orientation behaviour of *T. castaneum* (Coleoptera: Tenebrionidae). Bulletin of Entomological Research 80, 443–451.
- Obeng-Ofori, D., 1991. Analysis of orientation behaviour of *Tribolium castaneum* and *T. confusum* to synthetic aggregation pheromone. Entomologia Experimentalis et Applicata 60, 125–133.
- O'Ceallachain, D.P., Ryan, M.F., 1977. Production and perception of pheromones by the beetle *Tribolium confusum*. Journal of Insect Physiology 23, 1303–1310.
- Olsson, P.O.C., Ryne, C., Wallen, R., Anderbrant, O., Lofstedt, C., 2006. Male-produced sex pheromone in *Tribolium confusum*: behaviour and investigation of pheromone production locations. Journal of Stored Products Research 42, 173–182.
- Phillips, T.W., Jiang, X.-L., Burkholder, W.E., Phillips, J.K., Tran, H.Q., 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.
- Phillips, T.W., Cogan, P.M., Fadamiro, H.Y., 2000. Pheromones. In: Subramanyam, B., Hagstrum, D.W. (Eds.), Alternatives to Pesticides in Stored-product IPM. Kluwer Academic Publishers, Boston, pp. 273–302.
- Phillips, T.W., 1997. Semiochemicals of stored-product insects: research and applications. Journal of Stored Products Research 33, 17–30.
- Romero, S.A., Campbell, J.F., Nechols, J.R., With, K.A., 2009. Movement behavior in response to landscape structure: the role of functional grain. Landscape Ecology 24, 39–51.

- Romero, S.A., Campbell, J.F., Nechols, J.R., With, K.A., 2010. Movement behavior of red flour beetle: response to habitat cues and patch boundaries. Environmental Entomology 39, 919–929.
- Romero, S.A., 2007. Influence of Landscape Structure on Movement Behavior and Habitat Use by Red Flour Beetle (*Tribolium castaneum*). Department of Entomology. Kansas State University, Manhattan, 148 pp.
- Ryan, M.F., O'Ceallachain, D.P., 1976. Aggregation and sex pheromones in the beetle Tribolium confusum. Journal of Insect Physiology 22, 1501–1503.
- Semeao, A.A., Campbell, J.F., Whitworth, R.J., Sloderbeck, P.E., 2012. Influence of environmental and physical factors on capture of *Tribolium castaneum* (Coleoptera: Tenebrionidae) in a flour mill. Journal of Economic Entomology 105, 686–702.
- Sokoloff, A., 1974. The Biology of Tribolium. Oxford Univesity Press, Oxford.
- Stejskal, V., 1995. The influence of food and shelter on the efficacy of a commercial sticky trap in *Tribolium castaneum* (Coleoptera: Tenebrionidae). Journal of Stored Products Research 31, 229–233.
- Suzuki, T., Sugawara, R., 1979. Isolation of an aggregation pheromone from the flour beetles *Tribolium castaneum* and *T. confusum* (Coleoptera: Tenebrionidae). Applied Entomology and Zoology 14, 228–230.
- Suzuki, T., Kozaki, J., Sugawara, R., Mori, K., 1984. Biological activities of the analogs of the aggregation pheromone of *Tribolium castaneum* (Coleoptera: Tenebrionidae). Applied Entomology and Zoology 19, 15–20.
- 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.
- Taylor, P.D., Fahrig, L., Henein, K., Merriam, G., 1993. Connectivity is a vital element of landscape structure. Oikos 68, 571–573.
- Thiemann, T., Nelms, B., Reisen, W.K., 2011. Bloodmeal host congregation and landscape structure impact the estimation of female mosquito (Diptera: Culicidae) abundance using dry ice-baited traps. Journal of Medical Entomology 48, 513–517.
- Verheggen, F., Ryne, C., Olsson, P.O., Arnaud, L., Lognay, G., Hogberg, H.E., Persson, D., Haubruge, E., Lofstedt, C., 2007. Electrophysiological and behavioral activity of secondary metabolites in the confused flour beetle, *Tribolium confusum*. Journal of Chemical Ecology 33, 525–539.
- Wiens, J.A., Schooley, R.L., Weeks, R.D., 1997. Patchy landscapes and animal movements: do beetles percolate? Oikos 78, 257–264.
- Willis, E.R., Roth, L.M., 1950. The attraction of *Tribolium castaneum* to flour. Journal of Economic Entomology 43, 927–932.
- With, K.A., Crist, T.O., 1995. Critical thresholds in species' responses to landscape structure. Ecology 76, 2446–2459.
- With, K.A., King, A.W., 1999. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. Landscape Ecology 14, 73–82.
- With, K.A., Pavuk, D.M., Worchuck, J.L., Oates, R.K., Fisher, J.L., 2002. Threshold effects of landscape structure on biological control in agroecosystems. Ecological Applications 12, 52–65.
- Zar, J.H., 1999. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, NJ.