Partial Disturbance of Resources Foraged by *Reticulitermes flavipes*[†]

by

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ABSTRACT

The introduction of termiticidal baits over 10 years ago has increased interest in the basic foraging behavior of pest termite species. Due to the amount of interference with foraged cellulose material (bait matrices, both treated and untreated) in bait stations as part of some control programs, the following study was initiated to examine the response of termites to very short term (1 wk) partial disturbances of a foraged resource. Does weekly interruption (disturbance) of 0, 25, 50, 75, or 100% of a foraged resource reduce feeding (or activity) by subterranean termites? Four pre-weighed cubes of southern yellow pine (*Pinus* spp. L.) in close proximity (1 cm) were provided to groups of Eastern subterranean termites [*Reticulitermes flavipes* (Kollar)] as foraging choices in two different screw-top jar arena tests. The first study was done in single jars requiring termites to stay confined near the disturbed blocks, while a second study used three connected jars providing the termites with the ability to avoid the jar with the disturbed blocks altogether. Both studies used similar methods, differing only in arena design. In these studies, one, two, three, all or none of the blocks were picked up carefully and the number of termites on the moved block counted weekly. Data from both studies indicated that termites did not permanently leave disturbed blocks, and that between 50 and 75% of the blocks needed to be moved to reduce feeding on the disturbed blocks.

Keywords: termites, Eastern subterranean termites, disturbance, behavior, foraging

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INTRODUCTION

While soil applied termiticides remain the primary source of termite control in the United States, a number of pest management companies are using baits as a control measure (Su and Scheffrahn 1998; Grace and Su 2000). Traditionally, bait applications are made to an infested feeding station designed to accept both an untreated wooden resource (originally) followed by a treated cellulose resource (after discovery by termites). Some stations allow for the placement of multiple pieces of the untreated wooden resource. The purpose of multiple pieces is to minimize the effects of disturbance on the feeding termites. For those stations where removal of less than the total number of untreated wooden resources is possible this may be a valid concern.

Affinity to a feeding station is important in termite baiting, due to the nature of the control method. To have any influence on a colony, a large number of workers have to visit and remove quantities of toxicant. Only then can the toxicant be expected to manage the population at all (Esenther and Beal 1974). If the disturbance of a station, whether from checking for termite activity, or from replacing the untreated resource with toxicant-laden material, results in a long-term reduction of termite foraging at that station, then the management of the population is likely to be ineffective.

Disturbance has long been of interest to those studying termite behavior. Laboratory studies have examined disturbance to foraging termites using a range of methods, including vibration (Hu *et al.* 2003) and puffs of air (Schwinghammer and Houseman 2006). Other studies have examined termite communication resulting from disturbance events (Stuart 1968; 1988).

This study addresses bait station disturbance in more general terms rather than the comparison of commercially available bait stations. The question is whether partial removal of foraging resources diminishes the affinity of termites to a foraged resource. The work described here is part of an overall examination of the influence of disturbance on termite activity and foraging affinity. In particular, this experiment focused on movement of partial foraging resources, asking what percentage of a resource can be disturbed without loss of termite foraging to the resource as a whole. Due to the short-term nature of the disturbance regime for this study, the test was run in a laboratory. The hypotheses are: Termites will not abandon a foraged resource if any part of it is disturbed (null). Termites will only abandon a resource when a certain percentage of the resource is disturbed (alternative).

The Eastern subterranean termite, *Reticulitermes flavipes* (Kollar) is a widely distributed pest species native to the Southeastern United States (Kofoid 1934). This species is a common target in pest control programs, both with soil-applied termiticides and with termiticidal bait applications. Due to its economic importance, this species was chosen as the candidate for this study.

METHODS AND MATERIALS

Termites.

Termites were collected from infested fallen timber on either the John W. Starr Memorial forest, or the Noxubee Wildlife Refuge, both within 10 miles of Starkville, MS. Infested timber was cut into 0.3-0.5 m sections and returned to the laboratory in galvanized steel garbage cans (30 gal, ~114 L). Termite-infested sections remained in the cans in the laboratory at ambient temperature (~22-24°C), for no more than three months prior to extraction. *Reticulitermes* spp. termites are common in these areas, and the termites were identified as *R. flavipes* using morphological characters described in Hostettler *et al.* (1995).

Cubes of southern yellow pine (*Pinus* Linn. spp.; 1.3 cm per side) were autoclaved (solids setting, 45 min), dried in an oven at 90°C for 24 hrs, cooled for 1 hr in a desiccator containing drierite (~1-3 % R.H.), and initial dry mass recorded (to 0.01 mg) for each block used in the study. After the completion of each trial this process was repeated (except for autoclaving) and final dry masses recorded for each block. The difference between these masses (mass loss) was calculated and analyzed (see below). Late in this project a second study was added to examine the effects of spatial separation on termite feeding at disturbed blocks. The details of both studies are considered separately below.

First Study: Arenas.

Arenas for this study consisted of plastic screw-top jars (10 cm × 8.5 cm). The jars were filled with dry silica sand (150 g; Fisher Scientific, Fairlawn NJ), and then moistened with deionized water (27 ml). Each jar was provided with four pine blocks labeled A-D in pencil (prepared as described above), arranged in a square on an aluminum foil square measuring 5 cm per side (marked for block locations in pencil; Fig. 1). Finally, 200 termites (198 workers and 2 soldiers) were added to each jar, closed and placed into an unlit 25 ± 1°C incubator (~87 % R.H.).

Second study: Arenas.

Rather than confining termites to a single jar in which only some blocks were disturbed, this study used three jars (same size as above) connected by plastic tubing at the bases (Fig. 2). The arenas for this study were identical to

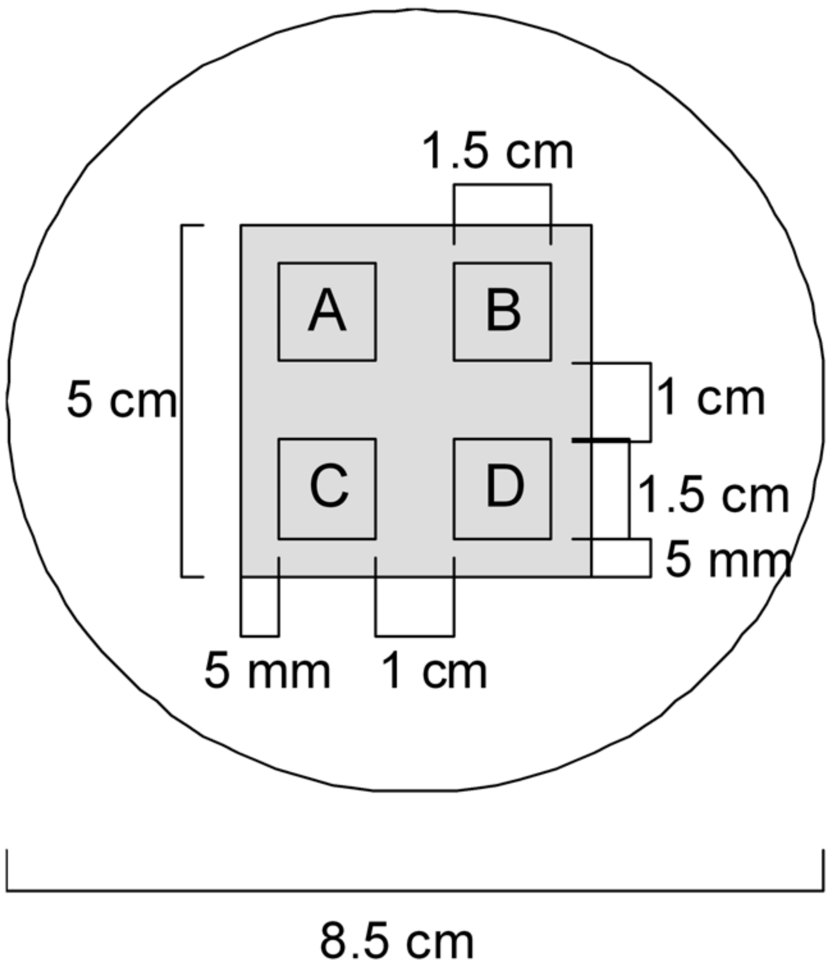

Fig. 1. Top view of the jar arenas used in the first study. The center of the diagram shows the aluminum foil sheet used to provide locations for the foraged blocks.

those used by Woodrow *et al.* (2008), including the use of drinking straws to create tunnels leading to the tubing. Each outer jar was prepared exactly as described above, with the foil squares moved such that they did not cover the sand tunnels. The center jar contained only moistened sand. All jars contained 150 g Silica sand (Fisher) moistened with 27 ml of deionized water. Once arenas were attached to the fiberglass boards (20.32 x 40.64 cm), the board was labeled with treatment, experimental unit, and the outer jars assigned as "side 1" (left) and "side 2" (right). Arenas were placed into one of three 25±1°C incubators, maintained at ~80% R.H. There were five experimental units of each treatment and each incubator contained at least one unit per treatment (Table 1). As in the first study, dried, pre-weighed blocks were placed in their positions in both outer jars (four each), and the 200 termites (198 workers and 2 soldiers) were released in the center jar.

Table 1. Experimental design describing which blocks in the available resource were moved each week.

Treatment	% Resource Disturbed	Description
1	25	A block moved each week
2	50	A and B blocks moved each week
3	75	A, B, C blocks moved each week
4	100	All blocks moved each week
5	0	No blocks moved each week

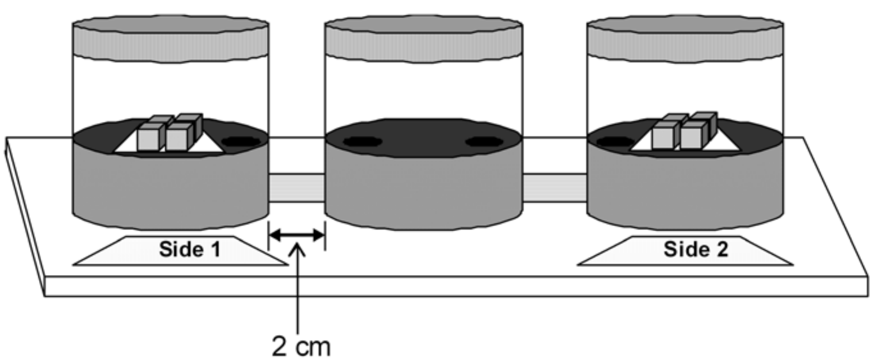

Fig. 2. Side view of the three-jar arenas used in the second study (after Woodrow *et al.* 2008). Blocks in outer jars were arranged as shown in Fig. 1. Black ovals indicate holes leading to the plastic tubing connecting the jars.

Experimental design (both studies).

The treatments in both experiments were based on the percentage (0, 25, 50, 75, or 100%) of the total foraging resource moved on a weekly basis (Table 1). In the second study, only the blocks in side 2 were disturbed (according to Table 1, same treatments), the blocks in side 1 were left undisturbed. In the first study, three colonies of *R. flavipes* were used in separate trials. Each jar (or arena in the second study) was considered an experimental unit, and there were five experimental units per treatment.

Disturbance procedure (both studies).

Each week for four weeks, appropriate blocks were removed from each jar/arena, termites clinging to the block were knocked off into Petri dishes (labeled A-D) and counted, finally the block and termites were returned to the jar. Obviously, movement of blocks was impossible without first removing the lid from each jar. To accommodate this difference, jar lids (side 2 in the second study) were removed from control (0% block movement) units for ~30 sec. This lid removal, and all block movements were done at the same time each week. Blocks were returned to their previous locations in jars and the termites returned to one side of the jar (*i.e.*, not poured back onto a block). Termite number for each block was recorded separately for each jar at each weekly reading. For comparative purposes, a weighted statistic was created from these numbers to correct for the number of blocks:

Corrected Termite Number (CTN) = $(T_A + T_B + T_C + T_D) / BN$

Where T was total number of termites counted from a block (designated by subscript letter), and BN was the number of blocks removed for that particular treatment (*i.e.*, for the 75% treatment, BN = 3; Table 1). One recognized drawback to this approach for estimating termite activity is the lack of CTN data taken from the unmoved blocks (or side 1 blocks in the second study) at each time interval since the blocks must be moved (thus interfering with the actual treatment) to get an accurate termite count. Thus, CTN data provided an estimate of termite activity on the moved blocks over time, but could not provide the location of the remaining termites. While CTN data provided interesting information regarding termite movement, the block mass loss data provided a more useful test of the hypotheses.

At the end of four weeks (28 d), all jars were disassembled, blocks scraped clean of termites, excrement and sand, and placed in labeled Petri dishes for drying and final mass determination. Surviving termites were also counted to estimate the level of mortality from the study. While this study did not use mortality to make any inference about hypotheses, mortality data was recorded as it often provides an important estimate of the overall health of the study animals.

First study: Statistical analysis.

The null hypothesis stated that all percentages of food source disturbed on a weekly basis will have no influence on the number of termites visiting the block. The study collected two variables to test this hypothesis, CTN and mass loss of wooden blocks. For the null hypothesis to be true, all treatments must result in similar CTN for all time periods of the test. Testing for the alternative hypothesis (at least one of the percentages of food resource disturbance will effect termite visitation), was done by subjecting CTN values to repeated measures analysis using a mixed model in SAS with time period, treatment, replicate and colony as classification variables (SAS Institute 1985). CTN comparisons were made for all possible interactions of treatment and week with colony, replicate and treatment by colony interaction considered as random effects in the mixed model. An autoregressive correlation structure [AR(1)] was assumed for the repeated measures. Means were separated using Least Square Means (Tukey-Kramer adjustment; SAS Institute 1985).

Similar to CTN, rejection of the null hypothesis requires that at least one of the experimental treatments results in a significant mass loss difference between the moved and unmoved blocks. To correct for slight variations in original block mass (mean ± SEM: 1.11 ± 0.01 g; n= 300), percentage mass loss was used as the analysis variable. These data were analyzed using a mixed model in SAS with movement (of individual blocks), treatment, replicate and colony as classification variables (SAS Institute 1985). Percentage mass loss was compared in the treatment by movement interaction, with colony, replicate, and the colony by treatment interaction as random effects in the mixed model. Contrasts of movement, treatment, and their interaction were made for the 25, 50 and 75% movement treatments, as well as an estimate comparing the 0 and 100% movement treatments (SAS Institute 1985). Significance was reported for both CTN and percentage mass loss data at the 0.05 level unless otherwise noted.

Second study: Statistical analysis.

The lack of a colony effect in the first study led to using only one colony for the second study. The following hypotheses were examined using the block mass loss data (as percentage mass loss); 1) are there significant differences between mass lost by undisturbed blocks in each side (*i.e.* does being near disturbed blocks diminish feeding by termites)?, 2) was there a significant difference between disturbed blocks in side 2 and undisturbed blocks in side 1 (did termites feed more at a location distant from the disturbed blocks)?, and finally 3) was there a significant difference in mass lost by disturbed blocks and undisturbed blocks in side 2 (did termites feed more on nearby undisturbed blocks)? These hypotheses were tested using contrasts of the appropriate percentage block mass losses within treatments (SAS Institute 1985). Additional contrasts compared block mass loss between moved and unmoved blocks within the 100% moved treatment, and between unmoved blocks in the 0% moved treatment (effectively side 1 *vs.* side 2 for both comparisons). One final overall comparison was made using T-tests (SAS Institute 1985) of the combined percentage mass losses by jar (moved and unmoved block loss; side 1 vs. side 2) within treatments. CTN activity data in the second study were collected for side 2, and analyzed as described for the first study (above).

RESULTS

First study.

Separated by colony and treatment, mean mortality (± SEM) data ranged from 10.40 ± 0.77 (colony B, 75% treatment) to 17.5 ± 2.74 % (colony A, 100% treatment). With treatments combined, the mean mortalities for termites from each colony were: 15.84 ± 0.71 % for colony A, 12.88 ± 0.59 % for colony B, and 11.70 ± 0.71 % for colony C.

The influence of time of observation was the only fixed variable to significantly influence the corrected termite number (CTN) data (dF = 3, 167; F = 3.87; *P* = 0.0104). The effects of treatment (dF = 3, 167; F = 1.29; P = 0.3613) and the treatment by time interaction (dF = 3, 167; F = 1.41; P = 0.1878) were not significant. None of the random effects (colony, replicate, and treatment by colony interaction) significantly influenced the CTN data, thus the only significant differences in CTN were due to time of observation.

These data (with colonies combined) are presented in Fig. 3. In general, CTN values increased over time for all treatments. The CTN data for the 25% moved treatment was significant from 0 for weeks 2, 3 and 4 [dF = 167 (all weeks); t = 3.37, 3.01, 2.30; P = 0.0009, 0.0030, 0.0229 (weeks 2, 3 and 4 respectively); see Fig. 3]. CTN for the 75% moved treatment was significantly different from 0 at the 0.1 level for week 4 (dF = 167; t = 1.67; P = 0.0959; see Fig. 3). The 100% moved treatment was significantly different from 0 for week 4 as well (dF = 167; t = 2.57; P = 0.0112; see Fig. 3).

As with the CTN data, none of the random effect variables (colony, replicate, and colony by treatment interaction) significantly influenced percentage mass loss in this experiment. The percentage mass loss data are presented (colonies combined) in Fig. 4. Contrasts comparing the effects of movement status of blocks and treatments, excluding the 0 and 100% movements to form a complete factorial arrangement, showed that the main effects

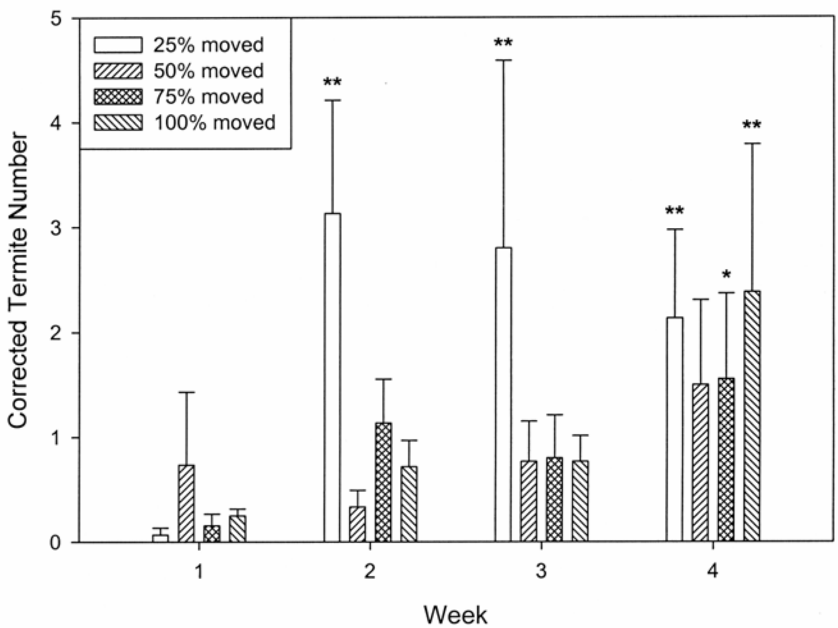

Fig. 3. Bars represent corrected termite numbers (CTN; termites per moved block) for each treatment by week of the first study (colonies combined; note that the 0% moved treatment has no CTN observations). Asterisks indicate significant comparisons within treatments (among weeks) made via mixed model analysis for repeated measures. Single asterisks represent significance at the 0.1 level, while double asterisks indicate significance at the 0.05 level.

of movement status and treatment were not significant, but the interaction was significant in impacting percentage mass loss (dF = 2, 219; F = 3.19; *P* = 0.0431). The comparison between the 0 and 100% moved treatments indicated no significant difference between them (dF = 219; t = -0.26; *P* = 0.7961). Teasing apart the movement by treatment interaction showed that only the 50% moved treatment had a significant difference between the moved and unmoved blocks (dF = 1, 219; F = 4.45; *P* = 0.0342; see Fig. 4), and that there were no significant differences among the unmoved blocks collectively or the moved blocks collectively [dF = 3, 219 (for both); F = 1.45, 0.82; *P* = 0.2279, 0.4832 (for unmoved and moved blocks respectively)].

Second study.

All data from three experimental units (one from the 25% moved, and two from the 0% moved treatments) were removed from this study due to excessive termite mortality (100, 100, and 43% respectively). The overall mean (±SEM) mortality for the study was 22.91±1.04 %, and termite mortality

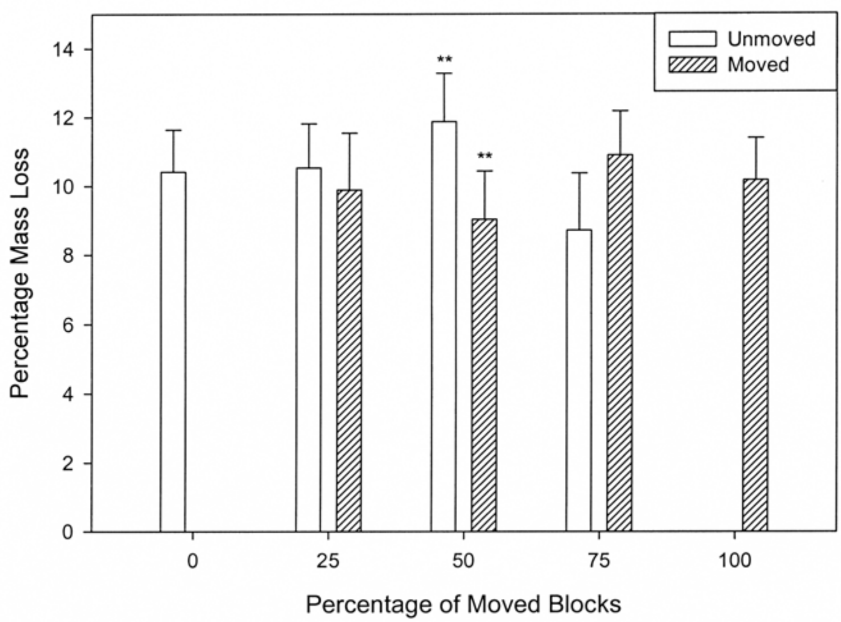

Fig. 4. Bars represent percentage mass loss for each treatment in the first study (with colony data combined), separated into moved blocks and unmoved block data. Comparisons between moved and unmoved blocks were made via contrasts. Double asterisks indicate significance at the 0.05 level.

was not significantly different among treatments (dF = 4, 21; F = 0.33; P = 0.854), as determined by analysis of variance (Minitab Inc., 2007).

Means (±SEM) of CTN separated by treatment and week (for all treatments save the 0% movement treatment) are presented in Fig. 5. No significant differences were found among the fixed effects in the mixed model analysis of CTN. As before, only the 25, 50, 75 and 100% movement treatments could be analyzed for CTN as data from the 0% movement treatment could not be measured accurately. One replicate (from the 25% movement treatment) was removed from the CTN data set due to excessive mortality as noted above. Fixed effects included time of observation (dF = 3, 45; F = 1.00; P = 0.4022) and the time by treatment interaction (dF = 3, 45; F = 0.86; P = 0.5702). Among the individual comparisons, only the interaction of the 75% moved treatment on the fourth week was significant (dF = 3, 45; t = 2.90; P = 0.0057).

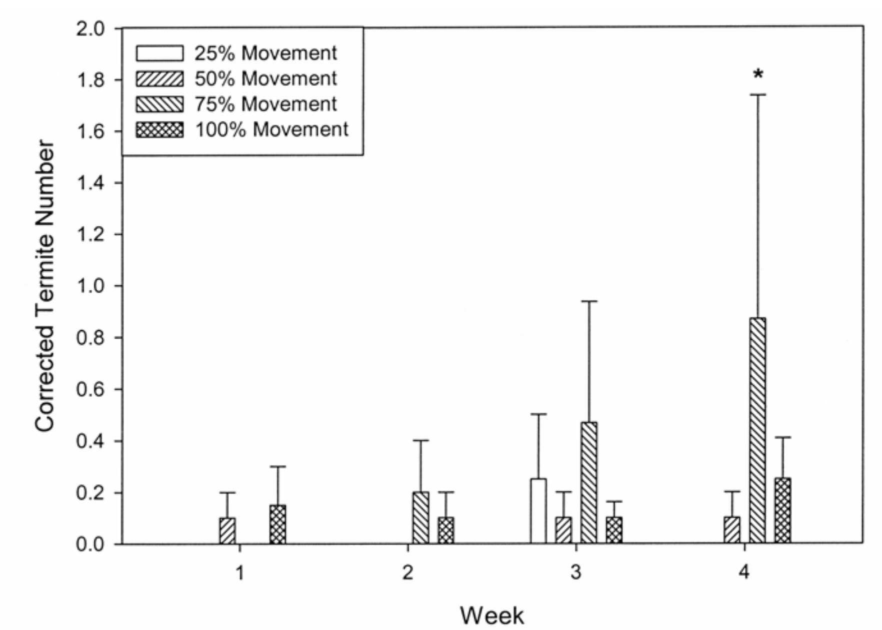

Fig. 5. Bars represent corrected termite numbers (CTN; termites per moved block) for each treatment by week of the second study (note that the 0% moved treatment has no CTN observations). A single asterisk indicates a significant comparison (at the 0.05 level) within treatments (among weeks) made via mixed model analysis for repeated measures.

Three contrasts were made for the block mass loss data in the 25, 50 and 75% movement treatments: 1) unmoved blocks in the control side vs. the treated side, 2) moved blocks on the treated side vs. the unmoved blocks on the control side, and 3) moved blocks vs. unmoved blocks on the treated side. Mean (±SEM) block mass loss data are illustrated in Fig. 6.

For comparison 1, the control side unmoved blocks had significantly greater (at the 0.1 level) block mass loss than the unmoved blocks on the treatment side (dF = 129; $t = 1.69$; $P = 0.094$) only in the 75% treatment. For the 25 and 50% treatments, no significant differences were found between block mass losses of the unmoved blocks in each side of the arenas.

For comparison 2, the control side unmoved blocks had significantly greater (at the 0.1 level) block mass loss than moved blocks on the treatment side (dF = 129; $t = 1.84$; $P = 0.0673$) only in the 75% treatment. For the 25 and 50% treatments, no significant differences were found between the moved

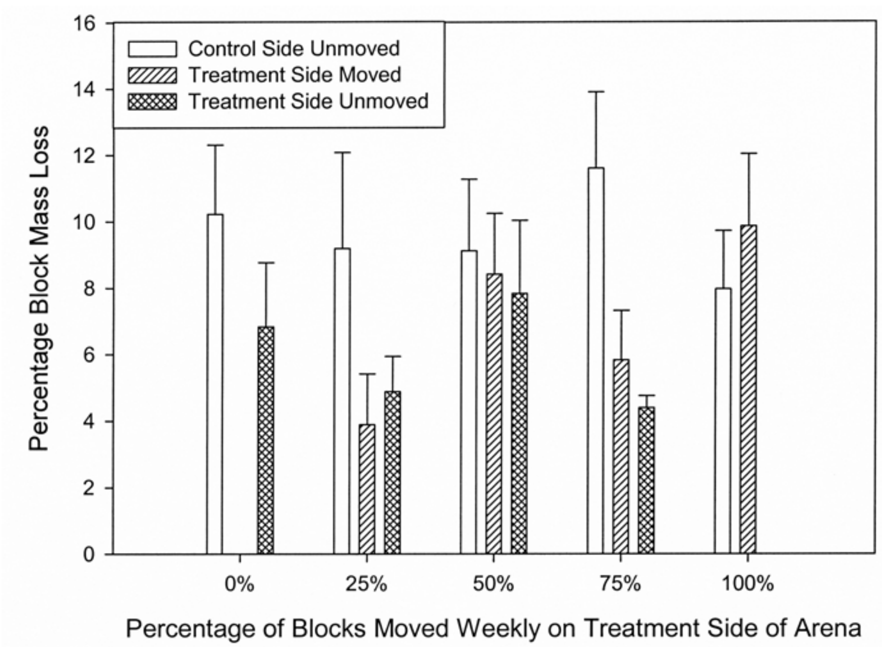

Fig. 6. Bars represent percentage mass loss for each treatment for the second study. Data are separated into moved blocks and unmoved blocks in the treatment side, and unmoved blocks in the control side of arenas.

block mass losses on the treatment side and the unmoved block mass losses on the control side.

For comparison 3, there were no significant differences in mass loss between the unmoved and moved blocks on the treatment side on the arenas for the 25, 50, or 75% treatments.

The overall comparison (combining moved and unmoved blocks) of the treatment and control jars (within treatments) indicated that only the 75% moved treatment had a significant difference between the mass lost by blocks in treatment (5.47 ± 1.12 %; side 2) jars and those in control (11.6 ± 2.29 %; side 1) jars (dF = 27.5; t = 2.41; P = 0.0229).

For both of the 0 and 100% movement treatments only one comparison was possible. For the 0% treatment, no significant difference was found between the unmoved blocks on each side of the arenas (dF = 129; t = 0.89; P = 0.3746). For the 100% treatment, no significant difference was found between the moved blocks on the treatment side and the unmoved blocks on the control side (dF = 129; t = -0.64; P = 0.5207).

DISCUSSION

While the results of the first study's CTN data analyses produced significant differences for the 25, 75 and 100% treatments over time (Fig. 3), these data did not support the alternative hypothesis that there was a percentage of a foraging resource that, when disturbed, would cause termites to abandon it. The CTN data from the second study (Fig. 5) also did not support that hypothesis; however activity during this study was minimal — CTN median value for all treatments when separated by week was 0, and moved blocks were free of termites in 75 to 90% of experimental units each week. The CTN data are really a snapshot of activity on the moved blocks taken during the weekly imposition of the treatment (movement of said blocks). In Figures 3 and 5, particularly for the 25% treatment (in Fig. 3; 75 and 100% treatments in Fig. 5) there is a trend of increased activity on these blocks over the course of the study. The possible reasons for this will be covered below.

The activity data represent only termite locations at a given time, and does not necessarily indicate termite feeding on a particular substrate. To measure feeding, some indication of wood consumption must be made either through mass loss or visual damage ratings (such as the ASTM standard; ASTM 2008).

Clearly, mass loss is more objective than visual inspections. The results of the percentage mass loss analyses indicated that the alternative hypothesis was supported at least for the 50% moved treatment (Fig. 4) in the first study, but only for the 75% movement treatment in the second study (Fig. 6) at a significance level of 0.1. This is also supported by the combined comparison of the block mass loss in control and treatment side jars, where the 75% moved treatment was the only significant difference found. The variation between the studies may be an artifact of the treatment percentages chosen for the study, since 0, 25, 50, 75, and 100% movement were chosen arbitrarily. This suggests that the actual value for the termite response may be between 50 and 75% movement of foraged materials. Alternatively, the differing results between the tests may suggest that the termites increase their willingness to accept disturbance of the blocks as their ability to move further from the disturbance increases (~20 cm in this case). Note that such movement may only be temporary as seen in the CTN data above, and also with other acute disturbance data from the literature (Hu *et al.* 2003; Schwinghammer and Houseman 2006).

If the alternative hypothesis were correct, it is expected that both a reduction in feeding on moved blocks at some point (25, 50, or 75%) would occur, as well as a reduction in feeding on moved blocks at all higher percentages of disturbance (*i.e.*, if the termites responded to 50% disturbance, it would be expected that they would respond to 75 and 100% as well). While an effect was seen at 50% and 75% depending on the study, this did not extend to the higher percentage treatments in either study (Figures 4 and 6). In the first study comparisons for the 100% moved resource were compared only to the 100% unmoved treatment, and in no cases were the two treatments significantly different (Fig. 4). Similarly, in the second study a comparison of the unmoved blocks on the control side with the moved blocks on the treatment side for the 100% movement treatment found no significant differences between them. An even division between the moved and unmoved portions of the resource was enough to reduce feeding on moved blocks in the first study, but movement of 75% of the blocks was required in the second study for a similar effect. However, both data sets (mass loss and CTN, from both studies) refute the idea that the termites actually left the moved blocks permanently.

There may be multiple possibilities for why there was no extension of this feeding reduction to the higher percentage of moved block treatments (and the increase in activity over time). One idea is that the disturbance events chosen for this study did not have severe consequences for the termites (moving the blocks is non-fatal), and thus may not have represented a sufficient stimulus to induce any avoidance response (*i.e.* the termites effectively did not take notice of the disturbance). This keeps with the goal of the study; examining non-fatal disturbances (simple movement) of foraged resources. Given the block mass loss differences noted at the 50 and 75% block movement treatments (depending on the study) this seems unlikely. Another idea is that termites did respond to the disturbance events but eventually became habituated to them (possibly quite quickly in the first study's 100% movement treatment, as there was no alternative food), which is consistent with the block mass loss differences noted above.

As with any study of stimulus-response behavior in animals, the possibility of eventual habituation to a stimulus, even during a short term experiment as described here may occur. Generally, habituation requires the capacity for learned avoidance of repellent stimuli (or vice versa for attractant stimuli) and the eventual ignoring of said stimuli after repeated exposures. It is possible that the repetition of the stimulus (especially given the lack of negative association) may have allowed the termites to ignore the disturbance over time (Figures 3 and 5). Future studies should counter habituation by using disturbance events with negative consequences, such as those involving dead nestmates (Fei and Henderson 2006; Woodrow *et al.* 2008). Habituation has been observed in studies of vibrational disturbance with *R. flavipes* (Hu *et al.* 2003). Habituation also occurs in *R. flavipes* workers in response to normally attractive semiochemicals, such as extracts from the brown-rot fungus *Gloephyllum trabeum* (Pers. ex Fr.) Murr. (Grace 1989). Goldberg and Grassé (1981) reported evidence of learning a simple maze by *R. lucifugus* (Rossi) workers exposed to the same maze previously (even when experienced termites are present as only part of an otherwise naïve group). Thus foraging in *Reticulitermes* spp. is far from a simple orientation event along temperature and semiochemical gradients towards possible food sources.

It appeared from the CTN analyses of both data sets that the null hypothesis could not be rejected. Both CTN data sets however, agreed with the idea that habituation to the disturbance event sequence (Figures 3 and 5) had occurred over time. Certainly there was little indication of termites abandoning the disturbed blocks over the course of these studies (Figures 3 and 5). As a result of the confounding effects of habituation (along with the snapshot nature of those observations), the mass loss data are more useful for testing these hypotheses.

In addition to the possibility of habituation is the possibly confounding factor of confinement. As with any laboratory experiment on animals, the arenas provided were obviously much smaller than the normal foraging areas of the termites tested. To an extent this is unavoidable, after all estimates of *R. flavipes* colony size vary from 240,000 (Howard *et al.* 1982) to 3.5 million individuals (Forschler and Townsend 1996), with larger colonies' foraging tunnels estimated to cover up to 1091 m^2 (Grace *et al.* 1989). Since no laboratory has this kind of internal space, all laboratory studies with termites suffer from confinement. In the first study, the confinement and limits on available food sources prevented complete abandonment of the foraged resource provided (at least in the 100% disturbed treatment). However, this problem was alleviated in the second study by providing termites with two easily accessed additional areas (one of which contained an identical set of food sources). From the percentage block mass loss data in these studies it appears that reductions in feeding due to disturbance may occur only when between 50 and 75% of the foraged resource is disturbed.

In these studies the movement treatments were repeated week after week, and the mass loss data are a collective measure of feeding over the whole 4-week period of the study, there was no way to differentiate damage to blocks on a weekly basis to avoid habituation to the stimulus during the successive weeks of the test. Perhaps a future study may need to involve destructive sampling to account for these problems.

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